Coloniality in the sociable weaver *Philetairus socius*

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The sociable weaver bird *Philetairus socius*

SUMMARY

The aim of the present study was to investigate the correlates (causes and consequences) of coloniality in the sociable weaver *Philetairus socius,* a highly colonial passerine resident in southern Africa.

To determine the social and genetic organisation of colonies, behavioural, nest content and ringing data were collected in central Namibia during three field seasons (1995-1998). Blood samples were analysed using microsatellite DNA profiling. To investigate the implications of coloniality for patterns of spatial population dynamics, all colonies in a 40 km^2 area were surveyed in 1997 and 1998.

Social and genetic organisation was complex. Approximately half of all broods were provisioned by two males and a female (the rest by pairs). Only one male in each trio gained paternity suggesting cooperative breeding rather polyandry. Relatedness between helpers and breeders was not determined. However, male fledglings were more likely to remain philopatric than females and average male, but not female, relatedness was higher within than between colonies.

Extra-group paternity (17% chicks) and intraspecific brood parasitism (6% chicks) did occur, but neither correlated with colony size. Some aspects of reproductive success did correlate with colony size. In large colonies: chicks were lighter; snakes visited more frequently (and robbed all active nests); and adult ecto-parasite loads were greater. However, based on mean reproductive success there was no net cost or benefit of being in large colonies.

Coloniality also influenced local population dynamics. Colony size **but not** isolation affected both colonization and extinction probabilities. Larger colonies were less likely to become unoccupied and more likely to be colonized. Intriguingly, both colony size **and** isolation affected the probability of a colony being occupied.

In conclusion, colonial living correlated with many aspects of sociable weaver biology. Priorities for future research include investigation of the relationships between social organisation, genetic structure and coloniality; and of patterns of spatial dynamics.

ACKNOWLEDGEMENTs

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Finally I would like to thank the four people who have, unrewarded, provided me with the emotional energy to complete this thesis. Throughout the duration of the study, my brother has relentlessly reminded me of the importance of considering alternative paradigms. Kes, with kindness, insight and her own inimitable determination, has fortified me in troubled times, been a joy on brighter days and (most concretely) devoted a week to reference collation, thus making time. My parents have given me support, encouragement, understanding, stimulation and often a roof for the last 26 years. I cannot thank you all enough.

CONTENTS

CHAPTER 1: GENERAL INTRODUCTION

1.1 GENERAL INTRODUCTION

The sociable weaver *Philetairus socius,* a small resident passerine of the arid regions of south western Africa, is remarkable for its sociality and the extent of its coloniality. Sociable weaver colonies comprise one or more, communally built and maintained, thatched compound nests. Each nests houses many birds in discrete chambers (Friedmann 1930; Maclean 1973; Collias and Collias 1978). Although the sociable weaver has been the subject of some behavioural research its social and mating system is only partially known (Friedmann 1930; Maclean 1973; Collias and Collias 1978). The aim of the present study is to use the extreme case of the sociable weaver to investigate the causes and consequences of avian coloniality, a field which has provoked much interest but little consensus in evolutionary ecology (Pulliam and Caraco 1984; Wittenberger and Hunt 1985; Siegel-Causey and Kharitonov 1990; Danchin and Wagner 1997).

1.1.1 Colonial living in birds.

Colonial bird species aggregate to form groups of pairs or individuals nesting in localised areas which they leave to feed (Wittenberger and Hunt 1985). Around 13% of birds breed in colonies but the frequency of coloniality varies dramatically across the class. Whilst 98% of marine species are colonial only 16% of passerine subfamilies include a colonial species (Lack 1968; Wittenberger and Hunt 1985; Siegel-Kausey and Kharitonov 1990). There is also considerable variety in the form of coloniality. For example, species vary in the seasonal timing of coloniality (breeding or non-breeding (Wittenberger and Hunt 1985)), the size of colonies (Brown and Brown 1996), and the existence of defended individual feeding territories (Emlen 1990).

Various general explanations have been proposed to explain the occurrence of coloniality (reviews: Wittenberger and Hunt 1985; Siegel-Causey and Kharitonov 1990; Brown and Brown 1996; Danchin and Wagner 1997). Perhaps most simply, individuals may be forced into a colonial distribution if essential resources, such as feeding areas (Wittenberger and Hunt 1985) or nesting sites protected from predators (Robinson 1985; Post 1994) are clustered. An alternative possibility is that colonies form to minimise travelling distance when birds feed at several different foraging grounds (Horn 1968). However, coloniality need not be the outcome of either resource or predator distributions alone (Alexander 1974). When individuals breed in colonies, passive group size effects (Foster and Treherne 1981;

Anderson and Hodum 1993) or active group behaviours, such as nest defence (Wiklund and Andersson 1994) or the transfer of information about foraging sites (Ward and Zahavi 1973; Brown and Brown 1996, but see Mock et al. 1988; Hagan and Walters 1990) may be important selective forces (Alexander 1974; Pulliam and Caraco 1984). More recently, interest has focused upon the possibility that colonies form as a result of increased potential for males (Møller 1987; Morton et al. 1990) or females (Wagner 1993; Wagner et al. 1996) to engage in alternative reproductive strategies (review: Birkhead and Møller 1992) when breeding densities are high. Alternatively, at a proximate level, colonies may form when potential recruits use conspecific presence or reproductive success as cues to settlement decisions (Reed and Oring 1992; Danchin and Wagner 1997).

1.1.2 Evolution and maintenance

No consensus has been achieved as to why coloniality evolves. There are two main reasons for this. First, coloniality may have evolved several times under the action of different selective pressures (Siegel-Causey and Kharitonov (1990) suggest at least ten separate origins among birds). Second, and more problematical, it is difficult to disentangle the evolution of coloniality from its current maintenance (Ward and Zahavi 1973; Siegel-Causey and Kharitonov 1990). In other words, a given species is colonial both because its lineage evolved coloniality and because coloniality is currently adaptive (assuming the absence of evolutionary constraints). This means that any explanation of the occurrence of coloniality in a species needs to include consideration of factors selecting for its initial evolution and those selecting for its current maintenance (Siegel-Causey and Kharitonov 1990). However, as colonial living influences many aspects of a species' social and physical environment (Birkhead 1985; Birkhead and Møller 1992; Brown and Brown 1996) discussion of the maintenance of coloniality implicitly includes both the consequences of coloniality (Hoogland and Sherman 1976; Brown and Brown 1996) and also the evolution of adaptations which may maximise any benefits or ameliorate any costs resulting from these consequences (Birkhead 1978; Siegel-Causey and Kharitonov 1990; Brown and Brown 1996). In order to formalise this problem Siegel-Causey and Kharitonov (1990) defined three types of factors involved in the evolution and maintenance of coloniality: (i) facilitating factors (which make it possible for coloniality to evolve); (ii) driving factors (those which select for the evolution of coloniality); and (iii) maintenance factors (those which post-date the initial evolution of coloniality but which now select for its current maintenance).

This layering of cause and subsequent adaptation makes it difficult or impossible to determine which factor or factors initially selected for the evolution of coloniality (Brown and Brown 1996). However, despite this difficulty, the correlates of coloniality (i.e. the causes and consequences of, and adaptations to, group living) are of general scientific importance both for the understanding of coloniality itself and in relation to the occurrence of disjunct groups of individuals in general (Pulliam and Caraco 1984; Koenig and Mumme 1987; Emlen 1997).

1.1.3 Correlates of coloniality

At a simple level, coloniality involves the aggregation of breeding individuals into clumps. Aggregation has two basic consequences. First, the local density of birds in colonies will be high. This may have implications for the local environment. It may also increase the frequency of interaction between conspecifics thus influencing the social environment and the evolution of behaviours. Second, if colonies are spatially discrete then, dependent upon the patterns of connectivity between colonies (i.e. the detail of inter-colony transfer), there may be implications for population structure and hence for population dynamics and population genetics.

1.1.4 High local-breeding densities

High local breeding densities may affect the local environment. For example by depressing the availability of resources (Alexander 1974), by attracting predators (Wittenberger and Hunt 1985; Wiklund and Andersson 1994), or by facilitating the transmission of parasites and pathogens (Alexander 1974; Brown and Brown 1996). If these effects have implications for fitness then adaptations may evolve to counter them (e.g. Ward and Zahavi (1973) explain the anti-predator adaptations seen in colonies as 'secondary' to the evolution of colonies as information-centres).

High local breeding densities also affect the social environment; individuals interact more frequently with conspecifics. Thus, high local breeding densities may influence the evolution of behaviours such as: communal vigilance (Hoogland and Sherman 1976; Hoogland 1979; Møller 1987; Brown and Brown 1996) and predator mobbing (Hoogland and Sherman 1976; Wiklund and Andersson 1994); transfer of information about patchy, ephemeral feeding sites (Ward and Zahavi 1973; Emlen and Demong 1975; Brown and Brown 1996); social signalling (Birkhead 1978); klepto-parasitism (Wittenberger and Hunt 1985) and feeding interference (Hunt et al. 1986); and infanticide (Møller 1987). Additionally, the absence of feeding territories (with some exceptions e.g. Emlen (1990)) and high

local density may influence mating systems and frequencies of extra-pair copulation (Morton et al. 1990; Birkhead and Møller 1992; Hoi and Hoi-Leitner 1997; Birkhead 1998) and brood parasitism (Brown and Brown 1996)). Some of these behaviours appear to be generally beneficial (e.g. communal vigilance, information transfer, social signalling) while the costs and benefits of others (e.g. kleptoparasitism, infanticide and extra-pair copulations) are likely to vary asymmetrically between age and sex classes (Møller 1987; Morton et al. 1990; Wagner et al. 1996).

1.1.5 Discrete breeding groups

The second general consequence of coloniality is that populations are divided into spatially discrete breeding groups. This division may create spatial structure in populations (especially when connectivity between groups is low) with important consequences for population dynamics and population genetics. These consequences are similar to those resulting from other factors generating spatial population structure, for example: social systems (Shwartz and Armitage 1980; Stacey et al. 1997); spatially discrete habitat patches (Smith 1980; Verboom et al. 1991; Sjoren Gulve 1994; Hanski 1999); or habitat loss (Hanski 1999). To date there have been relatively few studies of the spatial consequences of avian coloniality.

(a) Population dynamics

Much recent interest in population biology has focused on meta-populations; systems of local-populations connected by migration (Levins 1969; Hanski and Gilpin 1997; Hanski 1999). In such systems, the patterns of local-dynamics (extinctions and colonizations) determine the persistence of the meta-population (Levins 1969; Hanski 1999). Furthermore, the size and isolation of local-populations (or the habitat patches which could support them) often have important consequences for local dynamics; small local-populations are more likely to become extinct while isolated habitat-patches are less likely to be colonized (reviews: Hanski 1997, 1999).

When these spatial effects are included in simple models powerful predictions can be made about the frequencies of patch occupancy and turnover events (colonizations and extinctions) in real systems of habitat patches (Hanski et al. 1996; Hanski 1997, 1999). These predictions can be important for conservation projects (Lande 1988; Drechsler and Wissel 1998). Additionally spatial structure in population dynamics has implications for population genetics (Whitlock and McCauley 1990; Hedrick and Gilpin 1997; Giles and Goudet 1997) and for the

evolution of migration rate and other traits (Barton and Whitlock 1997; Olivieri and Gouyon 1997). Spatial structure may also stabilise host-parasite interactions (Nee et al. 1997) with consequences for the coexistence of diseases and their hosts in meta-populations. Therefore, if colonies act as local-populations connected by migration there may be important consequences for the biology of colonial species.

(b) Population genetics

The division of populations into discrete sub-populations may lead to spatial variation in the frequency of genes and the occurrence of genetic differentiation between sub-populations (Hedrick 1985). However, gene flow between sub-populations (generally mediated by dispersal) will be crucial in determining the extent of any genetic consequences of coloniality (Slatkin 1985). When rates of gene flow are low then sub-populations may become genetically differentiated from each other either as a result of neutral genetic drift (resulting from random sampling of gametes during sexual reproduction in small-subpopulations (Hedrick 1985)) or local adaptation in subpopulations (Dias and Blondel 1996).

There is some evidence to support greater genetic differentiation in colonial bird species. Barrowclough (1980) has reported higher levels of population level genetic variance (F_{ST}: Wright 1965) in colonial than in non-colonial species. However, the pattern is not consistent as some studies report significant genetic differentiation between colonies (Fleisher 1983; Avise et al. 1992) while others have found little or no genetic differentiation (Moen 1991). Differences in population sizes (Hedrick 1985), population histories (Hewitt and Butlin 1997) and rates of dispersal (Slatkin 1985) may explain much of this variation. Indeed, although increased population level genetic variance might be expected to elevate rates of evolution in colonial species, speciation is not more frequent in colonial lineages (Moers and Møller 1996).

Speciation is not the only potential consequence of population division. When colonies are small then low or sex-biased dispersal (Chesser 1991a,b) may lead to high levels of relatedness between group members and in particular between individuals of the philopatric sex (Chesser 1991a,b; Pope 1992; Morin et al. 1994; de Ruiter and Geffen 1998). Patterns of relatedness have considerable evolutionary significance. When relatedness between interactants is high, then altruistic behaviours may evolve, as the cost born by an altruist is discounted by their relatedness to the beneficiary (Hamilton 1964a). Therefore, altruistic behaviours are expected to be common in viscous populations (Hamilton 1964a; Kelly 1992; Queller 1992, Queller 1994). Similarly, patterns of relatedness are expected to have important consequences for the form of social and mating systems, especially when

parents and their adult offspring interact, as in many eusocial insects and cooperatively breeding birds (Keller and Reeve 1994; Emlen 1995, 1997; Bourke 1997).

1.1.6 Overview

Coloniality has evolved at least ten times in birds and it is possible that different factors have favoured its evolution in these different lineages (Siegel-Causey and Kharitonov 1990). It is difficult if not impossible to determine the historical cause of coloniality within a lineage, as studies of its evolution are confounded by current maintenance factors (Siegel-Causey and Kharitonov 1990; Brown and Brown 1996). However, the implications of group living are wide reaching and biologically important.

1.2 AIMS OF THE THESIS

The central aim of the present study is to investigate coloniality in the sociable weaver. Attention is focused on the maintenance, and two potential correlates, of coloniality in the sociable weaver.

(1) The main aim of chapter 2 is to investigate the general social organisation and mating system of the sociable weaver. This includes: (i) a description of the demography and social organisation of colonies; and (ii) the use of behavioural and genetic data to investigate the mating system of the sociable weaver. These data will provide the general context for understanding other aspects of the biology of sociable weavers.

(2) The main aim of chapter 3 is to investigate the maintenance of coloniality in the sociable weaver by determining how various hypothetical costs and benefits of coloniality vary with colony size.

(3) The main aim of chapter 4 is to investigate if coloniality imposes spatial structure on sociable weaver populations. If coloniality does impose spatial structure, then the dynamics of colony populations are expected to be determined by their size and position relative to other colonies.

(4) The main aim of chapter 5 is to investigate the consequences of coloniality and inter-colony movement for the genetic structure of the sociable weaver, and in particular for the patterns of relatedness within and between colonies.

1.3 STUDY SPECIES

The sociable weaver *Philetairus socius* is a small (27g), cryptically coloured, sexually monomorphic passerine of the semi-arid and arid regions of south western Africa (Maclean 1973; Figures 1.1, 1.2 (in Fig 1.1 distribution is based on Maclean (1973) and Clancey (1989))). It is highly social and inhabits large compound nest masses. These nests, which are communally built and maintained over many years, reach considerable sizes (upto: 7.5m by 4.6m by 1.5m) and can hold upto 500 birds (Friedmann 1930,1950; Maclean 1973; Collias and Collias 1978,1980). Besides their coloniality, sociable weavers are also remarkable for their low field metabolic rate and water influx; presumably physiological adaptations to their near desert habitat (Williams and Du Plessis 1996). Sociable weavers have a mixed diet of seeds and insects (Maclean 1973; Ferguson 1988).

1.3.1 General biology

(a) Colonies

Sociable weaver colony structures are composed of one or more nest masses (Friedmann 1930; Maclean 1973; Fig 1.2). Each nest mass is a compound nest made up of a superstructure (roof) and a substructure. The superstructure is generally of small twigs while the substructure consists of a thatch of straw (Maclean 1973). Entrance tunnels (upto 25cm in length) run from the lower surface of the nest mass to nest chambers (Fig 1.3). The nest chambers are roughly spherical (diameter of 15 cm) and are not interconnected (Maclean 1973). In the present study, to differentiate the physical nest from the social group, the term 'colony structure' is used to describe the nest masses inhabited by a colony of birds. When building the nest sociable weavers fill in old nest chambers and add new chambers beneath them (Maclean 1973). The thermal buffering provided by a sociable weaver nest is considerable. It provides protection from both high summer (Bartholomew et al. 1976) and low winter (White et al. 1975) temperatures.

Maclean (1973) described complex social organisation in the sociable weaver. He reported that the substructure is divided into social units (nest masses) and found that while the superstructure is a neutral area, birds are restricted to the substructure of their own nest mass. Furthermore, birds are faithful to their own nest mass within their colony from one season to the next and few birds move between colonies (Maclean 1973).

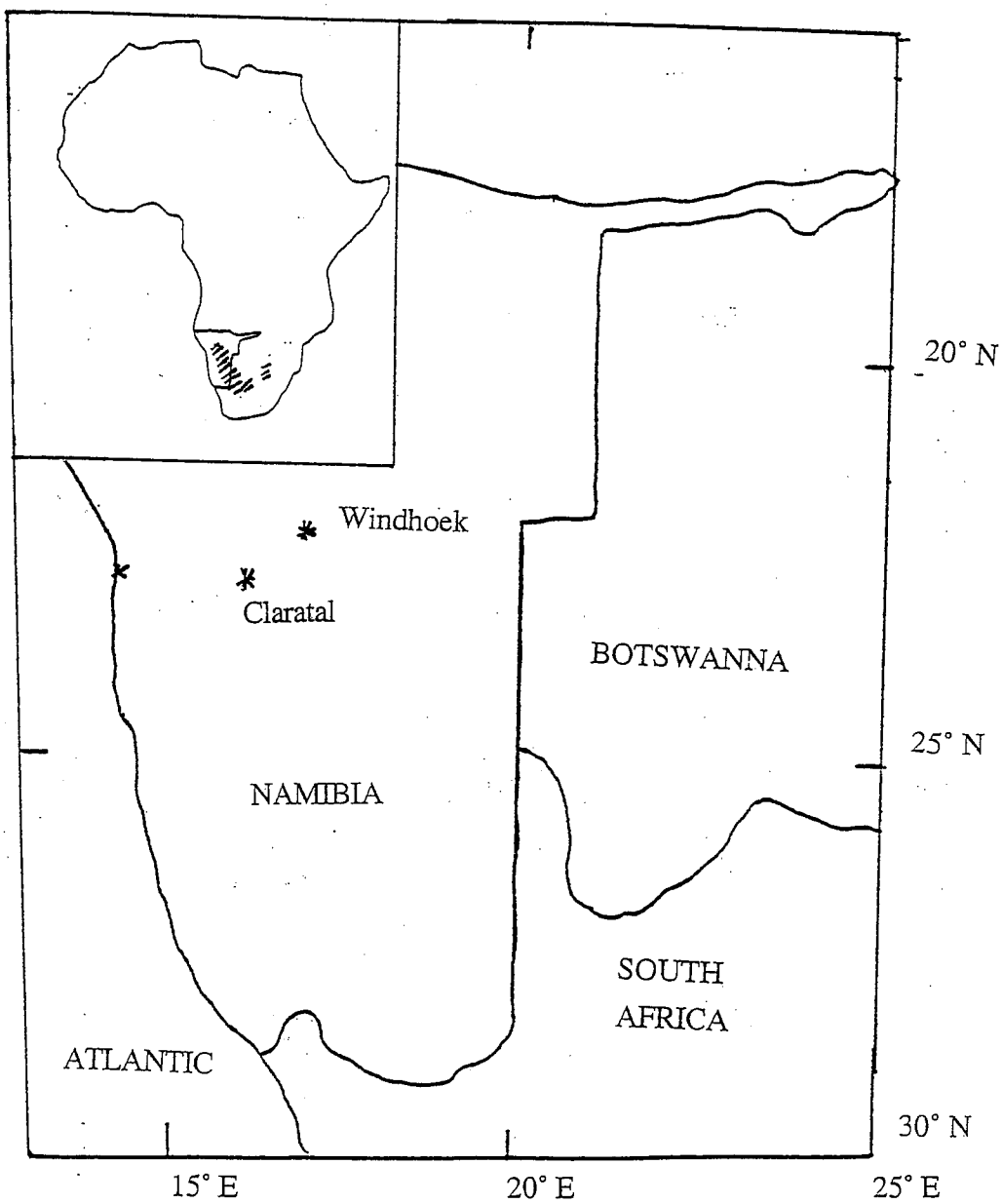
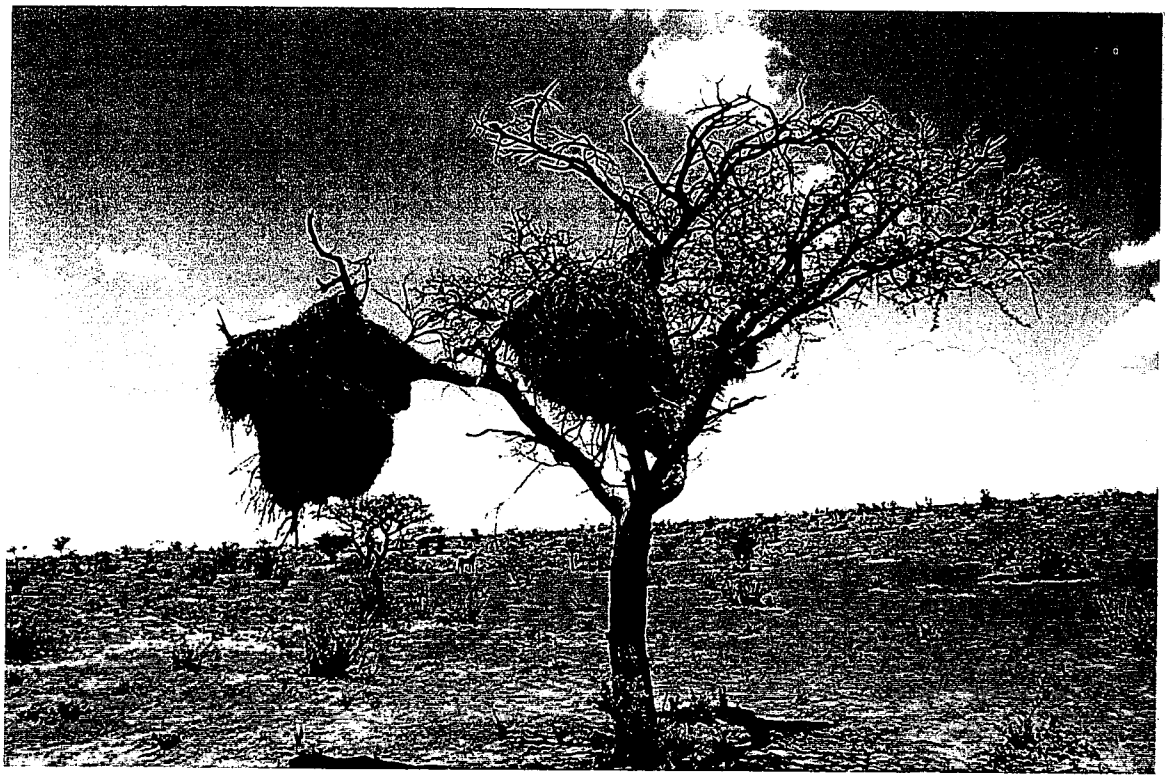


Figure 1.1. The study site Claratal Farm is in central Namibia. The smaller map shows the position of Namibia in southern Africa; and the distribution of the sociable weaver (shaded).

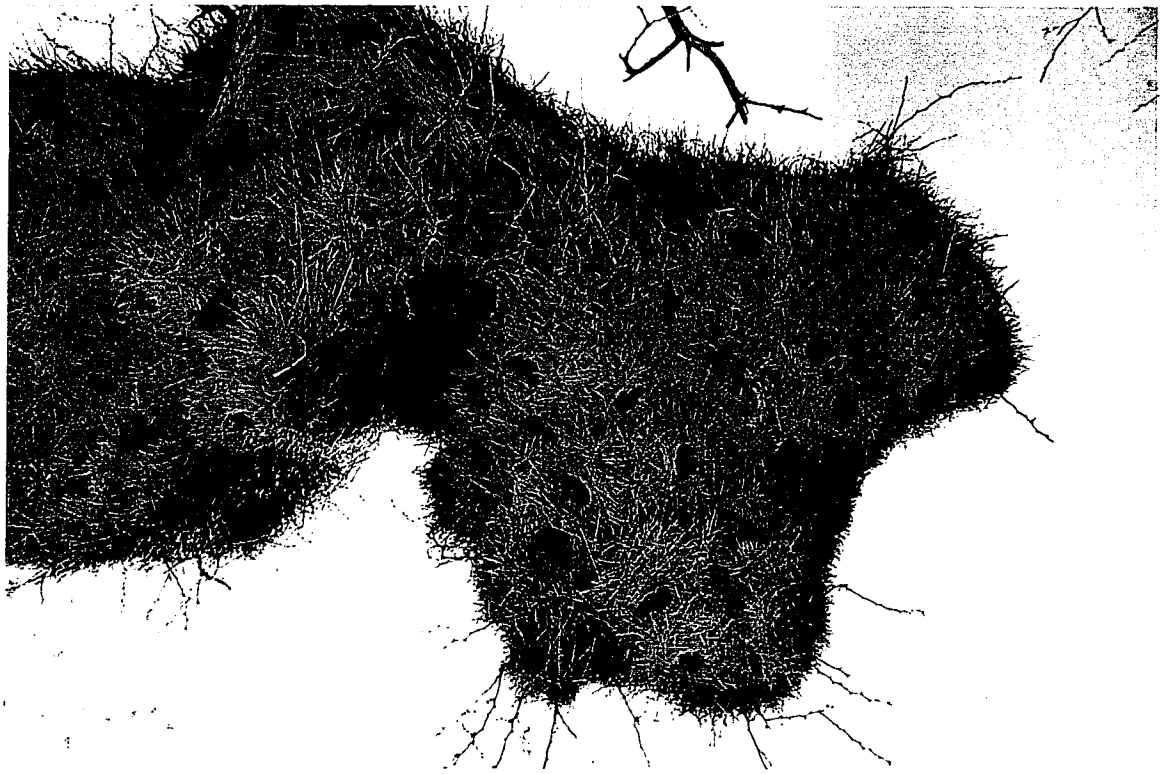
(a)



(b)

Figure 1.2 Sociable weaver colonies can be composed of one or more nest masses. Both (a) and (b) show colonies in camel thorn trees *Acacia erioloba*.

(a)



(b)

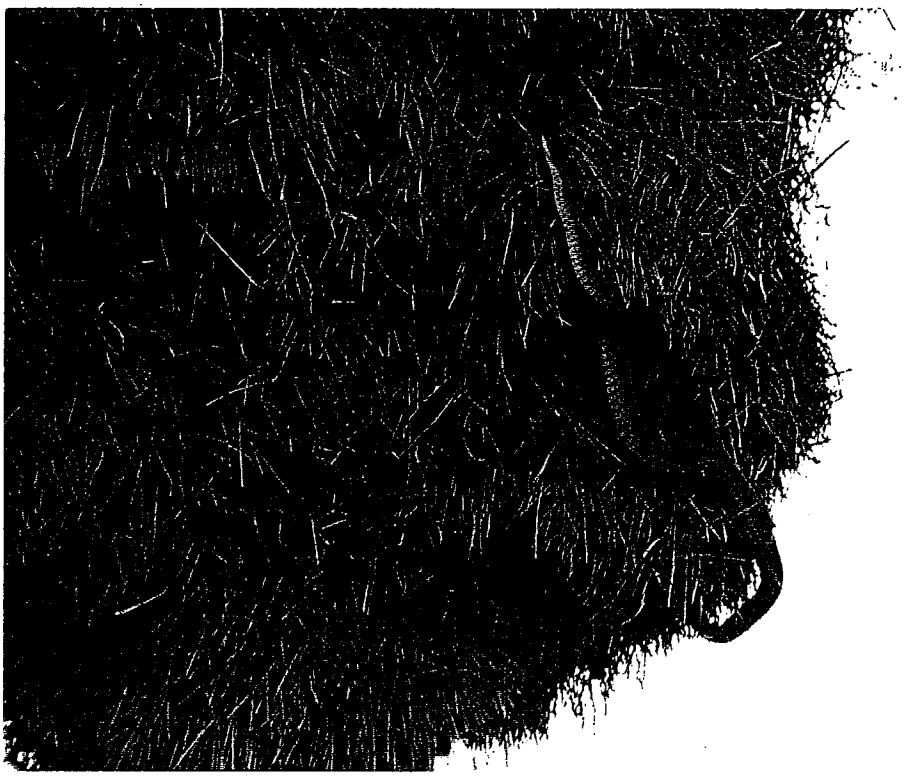


Figure 1.3 (a) Chamber entrances are clearly visible on the underside of a sociable weaver nest mass. (b) An adult boomslang *Dispholidus typus* prospecting for prey.

(b) breeding biology

Both the timing and extent of rainfall in the arid and semi-arid regions of south western Africa are unpredictable (Maclean 1973). Maclean (1973) reported that breeding in the sociable weaver commenced in response to rainfall or some associated factor; he recorded a lag of only six days between the first rains of the season and the first clutch laid. Breeding then continued for the duration of green plant growth following the rains with some birds producing four consecutive successful broods during a continuous nine month breeding period (Maclean 1973).

Although Maclean (1973) found that sociable weavers usually form monogamous pairs with males and females sharing incubation and provisioning, he observed that occasionally more than two adults provision the young. Additionally, when pairs lay several successive clutches fledglings from early broods help their parents to provision chicks in later broods (Maclean 1973).

In Maclean's (1973) study the average clutch size was 3.54 eggs (range: 2-6) and the average percentage of eggs producing successful fledglings was 13.1% (range for breeding periods: 3.1-17.8%). Average clutch size varied between breeding periods with fledging success following the same pattern (Maclean 1973). Sociable weavers suffer from considerable eggs and chick predation primarily by snakes (Maclean 1973; White et al. 1975; Fig 1.3b).

1.3.2 Taxonomy

Clancey (1989) has described four subspecies of sociable weavers varying slightly in colouring and size. The present study was carried out within the range of *P. socius eremnus* as defined in his 1989 paper.

The classification of the weaverbirds (family Ploceidae) has been a matter of some debate (Chapin 1917; Sushkin 1927; Bentz 1979). On the basis of mouth markings and skeletal features, Chapin (1917) included *Philetairus* in the sub family Ploceinae with the typical weavers. Sushkin (1927) disagreed. On the basis of the maxillo-palatine process he combined *Histurgops, Pseudonigrita, Plocepasser* and *Sporopipes* as a sub-family Plocepasserinae. Bentz (1979), using fore-limb musculature for his classification, placed Philetairus in the sub-family Passerinae with *Plocepasser, Pseudonigrita* and *Sporopipes* but also *Passer, Petronia, Montifringilla.* However he noted that *Philetairus, Plocepasser* and *Sporopipes* form a close grouping within the subfamily. The most recent classification (Sibley and Ahlquist 1990) based on DNA hybridisation temperatures, includes *Philetairus*

as a member of the family Passeridae, subfamily Ploceinae. They reject the inclusion of *Passer, Petronia* and *Montifrigilla* with *Philetairus* placing them in the subfamily Passerinae.

The sociable weavers closest relatives are the social weavers *Pseudonigrita spp.* of east Africa and the Sparrow weavers *Plocepasser spp.*. The grey capped social weaver *Pseudonigrita arnaudi* of east Africa and the white browed sparrow weaver *Plocepasser mahali* have been studied intensively (Collias and Collias 1978; Lewis 1982; Bennun 1989; Bennun 1992). Cooperative breeding occurs in both white browed sparrow weavers and grey capped social weavers. Like the sociable weaver both species live in groups. However unlike the sociable weaver neither species builds a compound nest.

1.4 STUDY SITE

The present study was carried out at Claratal Farm, Khomas region, Namibia (22.5°S, 16.5°E; Fig 1.1) with the kind aggreement of the owner, Mr E Freyer. The sociable weavers primarily built their colonies on camel thorn trees in wide valleys. Figure 1.4 shows the distribution of all active and inactive colony structures across the study site. Figure 1.5 shows the positions of the colonies used most intensively during the research.

The farm is in an arid region, the Khomas Highlands, situated close to the western edge of the sociable weavers distribution (Clancey 1989). Over the last 69 years (1929/30 - 1997/98), monthly rainfall at Claratal farmhouse has been recorded by the owner. During the period annual rainful has varied between 145 mm and 1015 mm with a mean of 354mm (Figure 1.6; based on the Mr Freyer's data set). Rains are concentrated during the austral summer (Figure 1.7; based on Mr Freyer's data set) with a short rainy period in November/December (which often fails) and main rains which start in January or February and last for three to six months. During the study period rainfall was close to average in one year and relatively poor during two years (185 mm, 365 mm and 237 mm in the first, second and third field seasons respectively).

During the dry season, with the exception of scattered trees and bushes (see Lovegrove 1993), there is little obvious plant life (Fig 1.8a), but following the start of the rains the sandy ground rapidly becomes covered with vegetation (Fig 1.8b). The survival of this plant growth, which supports the insects sociable weavers use to provision their chicks (Maclean 1973; Ferguson 1988), depends upon the frequency, amount and pattern of rainfall (E. Freyer, pers. comm.).

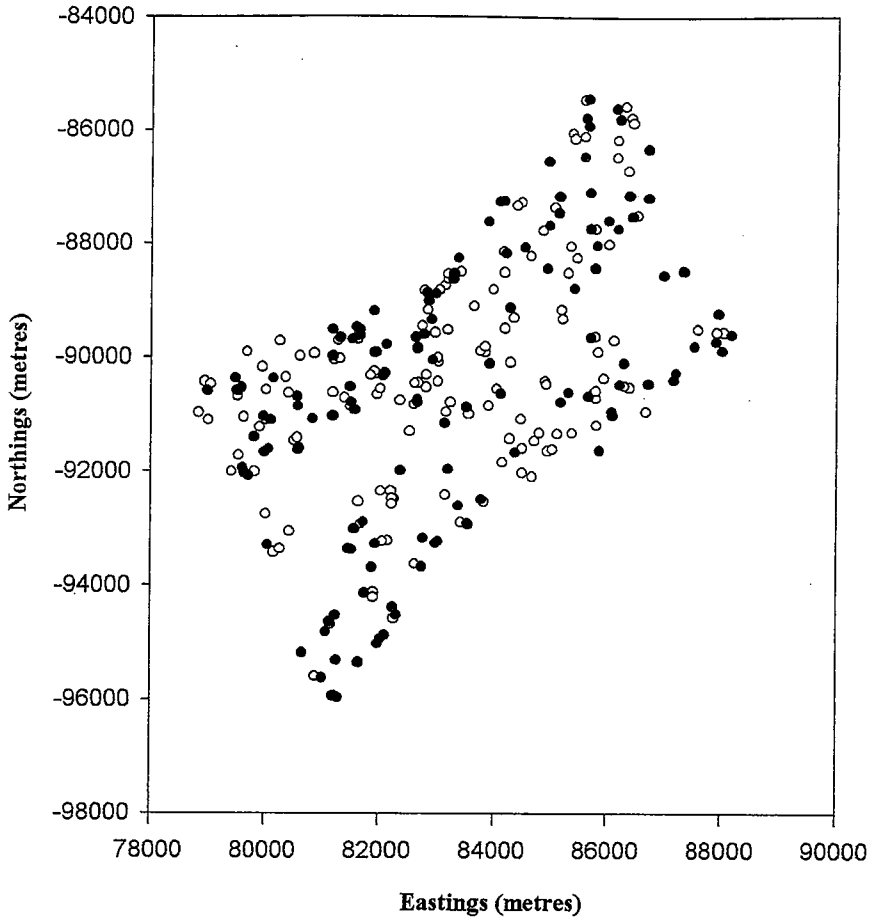


Figure 1.4 Spatial distribution of active (filled) and inactive (empty) sociable weaver colony structures at the Claratal study site. Distances are metres North and East of the point 16.000° E, 22.000° S.

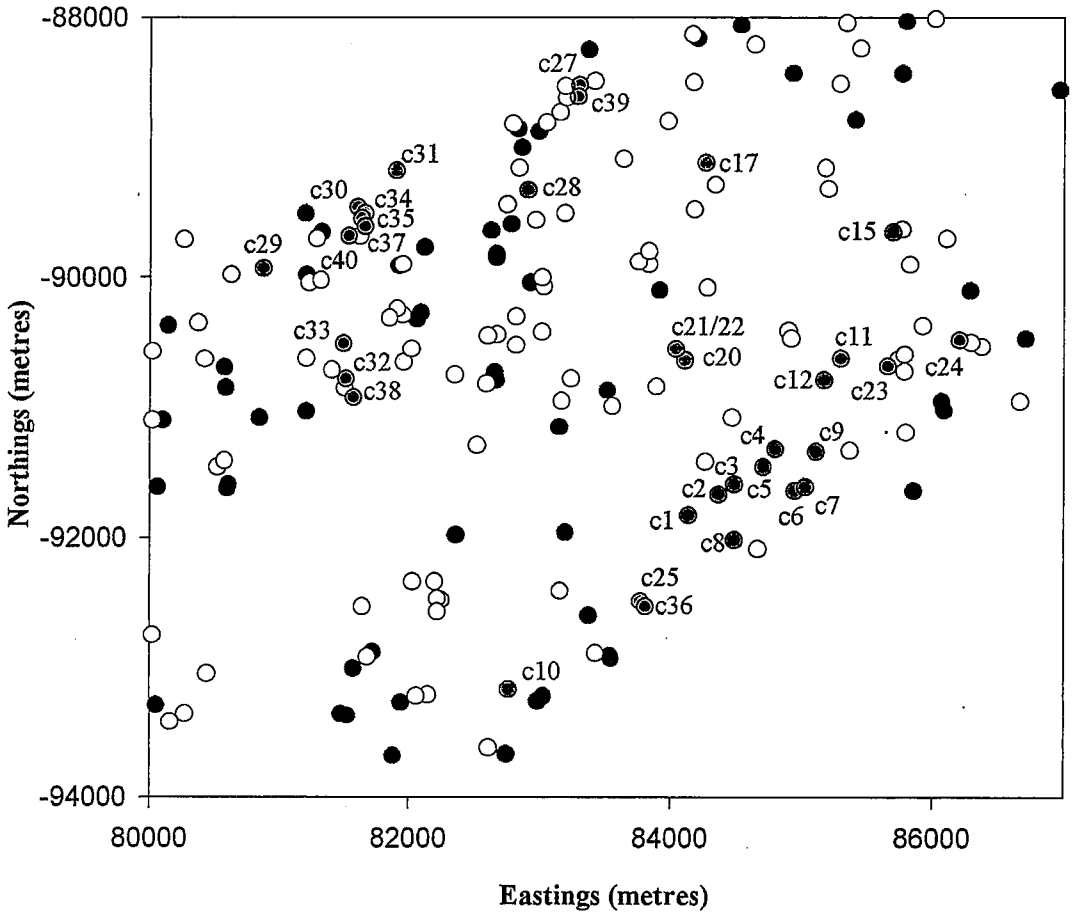


Figure 1.5 The positions of the colonies first ringed during the first (blue), second (red) and third (green) field seasons. Colonies which were active in 1998 but not used are shown as filled (black) circles. Colonies which were not used and were inactive in 1998 are shown as empty circles. Each colony was identified using a numeric code. Not all colonies were used for all types of data collection in every field season.

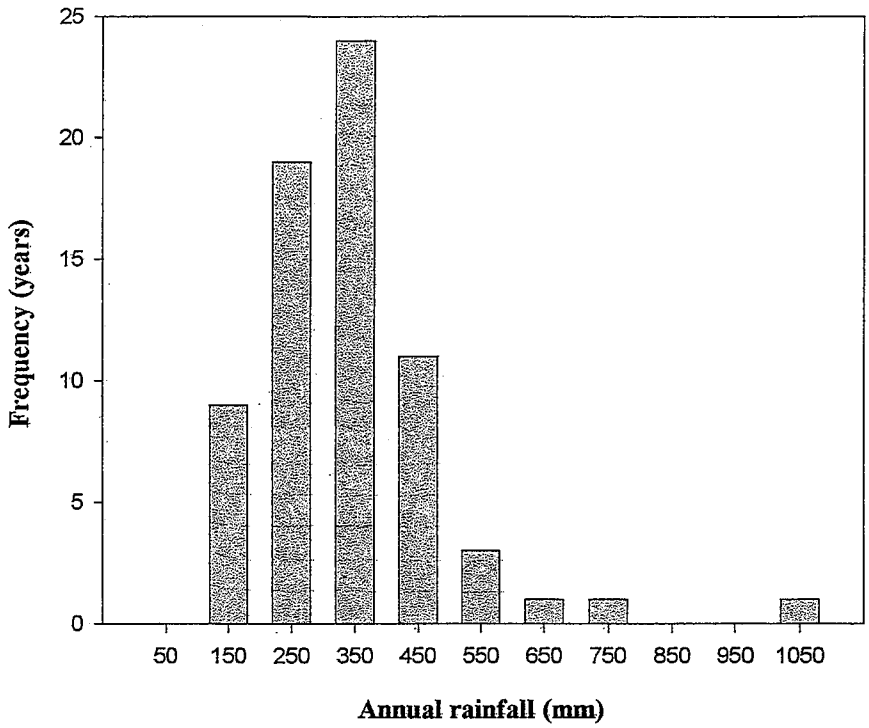


Fig 1.6 Frequency distribution of annual rainfall at the study site over the last 69 years. Annual rainfall is sorted into 11 classes each covering 100 mm (i.e. 1 - 100, 101 - 200 and so on). Over the 69 year period mean rainfall was 354mm. During the first, second and third years of the study annual rainfall was 185, 365 and 237 mm respectively.

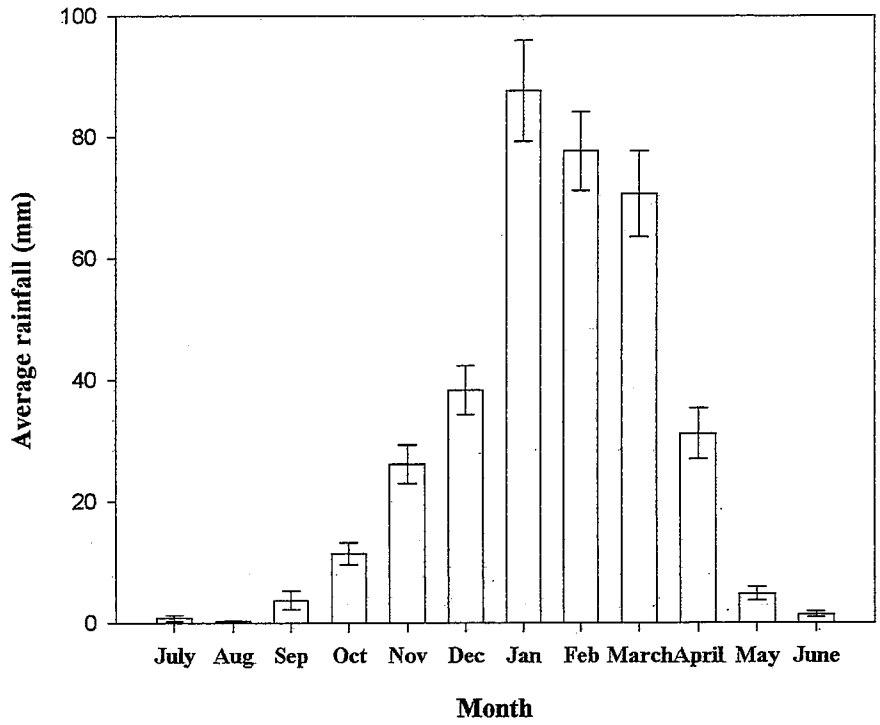


Figure 1.7 Pattern of average monthly rainfall at the study site over the last 69 years. Error bars are standard errors.

(a)

(b)

Figure 1.8 The study site: (a) at the end of the dry season; and (b) following a rainy season downpour.

1.5 GENERAL METHODS

Fieldwork was carried out during three field seasons. The first field season lasted from October 1995 until April 1996; the second from January 1997 until June 1997; and the third from November 1997 until May 1998. The timing and length of these field seasons was determined by the pattern of rainfall. Over the course of the study work was carried out on four main themes: (i) social organisation and mating system; (ii) variation in costs and benefits of coloniality with colony size; (iii) spatial structure and population dynamics; and (iv) patterns of relatedness within and between colonies. However to a greater or lesser extent all these themes were dependent upon several general methods presented in this section.

1.5.1 Capture of adults

Most adults were captured shortly before dawn using mist nets erected around the colonies. Some birds were captured in their chambers at night. One aluminium SAFRA numbered ring (cv - series) was used in combination with three coloured rings for behavioural identification. During the first field season plastic colour rings (A.C. Hughes) were used, but as these were not robust and many birds lost one or more, in the second and third field seasons anodized aluminium colour rings (A.C. Hughes) were used. In addition, unique combinations of up to three colours (W. H. Smiths acrylic paints: red, yellow, blue, green, white and black) were painted onto the foreheads and upper chest (three positions: left, centre, right) of captured individuals believed to be provisioning young. These markings facilitated the identification of individuals in the nest at night and in flight when provisioning.

At the time of capture three standard morphological measurements were made (mass: Pesola 50g balance, accuracy 0.5g; tarsus: calliper, accuracy 0.1 mm; wing chord: wing rule, accuracy 1.0 mm). Additionally, after pricking the brachial vein using a sterile hypodermic needle (0.5 x 25 mm), a small volume of blood (10-50 µl) was collected from each bird using an 80 µl capillary tube. The blood sample was evacuated into 1ml of absolute ethanol in a 1.5 ml screw top Ependorff tube using a rubber bulb and stored at ambient temperature.

During the third field season adult parasite load was assessed by holding birds (head out) in a polythene bag (245 mm x 160 mm) containing 5ml of ether (ethyl ethanoate) for 1 minute (Protocol: M. Du Plessis, pers. comm.). Three types of parasites were recorded (flies from the family Hippoboscidae; feather lice from the

family Pthiraptera; haematophagus mites). Hippoboscid flies, and haematophagus mites were difficult to capture and count in the field therefore only feather lice captured from adults were counted and used in further analyses.

1.5.2 Nest content checks

At each colony photographs and drawn plans were used to identify all nest chambers. All chambers of nine, eight and 15 colonies were checked during weekly nest checks in the first, second and third field seasons respectively. All eggs present in a chamber were numbered for identification. Egg length and breadth were measured (Calliper, accuracy 0.1 mm) and eggs from single or two egg clutches (assumed (Maclean 1973) to be unincubated) were weighed (Pesola 10g balance, accuracy 0.1g). These data showed it was possible to calculate an accurate index of fresh egg mass using breadth squared times length (linear regression $r^2 = 0.86$). Some clutches were predated or abandoned before the second nest check and were not included in analyses of clutch size. Chicks present in the nest were measured as for adults (Section 1.5.2). Once large enough, chicks were ringed and blood samples taken as for adults (Section 1.5.2). Tissue samples (brain) were collected from unhatched embryos and dead chicks. The number of parasites (blood sucking demestid larvae) on each chick was counted by visual inspection.

1.5.3 Statistical analysis

Statistical analyses followed Sokhal and Rohlf (1982) or Siegel and Castellan (1988). MINITAB (Version 11.12) was used for most analyses. Exceptions include the logistic regressions in chapter 4 which were performed using SPSS and the Mantel tests used in chapter 5 which were performed using GENETIX (Belkhir et al. 1998) following Manly (1997). Unless otherwise stated standard errors are given with mean values.

1.5.4 Licenses and permits

Research was carried out under study permits from the Ministry of Home Affairs, Government of Namibia and research permits from the Ministry of Environment and Tourism, Government of Namibia. Blood samples were imported into the UK under permit from the Ministry of Agriculture, Fisheries and Food.

CHAPTER 2: SOCIAL ORGANISATION AND MATING SYSTEM

2.1 INTRODUCTION

When attempting to understand a species from an evolutionary perspective, reproduction (the transfer of copies of an individual's genes to subsequent generations) is a key issue. As behaviours which maximise the transfer of an individuals genes are expected to be selected for, much interest in behavioural ecology has focused on the study of mating systems: the patterns of interaction between males and females during breeding attempts. These studies address two separate but closely connected issues: (i) The pattern of social association between breeding males and females. This includes the manner of formation, number and nature of bonds (Emlen and Oring 1977; Davies 1991), the form and degree of exclusivity of reproductive behaviours such as copulation and mate guarding (Birkhead and Møller 1992) and the occurrence and nature of parental care (Clutton-Brock 1991). (ii) The pattern of genetic outcomes of breeding attempts. The pattern of genetic outcomes describes the success with which individuals gain genetic parentage of offspring; the result of the cooperation and conflict outlined above.

The social organisation and demography of a species may have important consequences for the evolution of its mating system (Davies 1991) and the consequent pattern of genetic outcome (Birkhead and Møller 1992). This pattern of genetic outcome is of fundamental importance through its implications for both individual fitness (Davies 1991; Birkhead and Møller 1992; Chapter 3) and genetic population structure (Chesser 1991a,b; Girman et al. 1997; Chapter 5).

2.1.1 Mating systems: social associations and genetic outcomes

The patterns of social association between individuals of a species are strongly influenced by the dispersions of the two sexes and the degree of parental care necessary for successful reproduction (for review: Davies 1991). In general, as female reproductive success is more limited by the availability of essential resources than that of males (for whom mate limitation is more important), female dispersions are determined primarily by resource distributions while male dispersions respond to the opportunities to defend females or the resources females use. However, mating systems are not determined by resource distributions alone; the occurrence of parental care – dependant on the trade off between the costs and benefits of desertion (Maynard Smith 1977) – also influences the observed mating system.

A further important point is that all individuals are not of equivalent phenotypic quality. When male reproductive success is mate-limited some males may have a reproductive advantage, either as a result of their ability to defeat other males in intrasexual competition for mates or because they are preferentially chosen by females on the basis of sexually selected traits (Harvey and Bradbury 1991; Andersson 1994). These traits may signal the ability of males to provide females with direct benefits (e.g. Thornhill 1976) or good genes (e.g. Petrie 1994) or they may result from sensory biases (Proctor 1991) or runaway selection (Fisher 1958; O'Donald 1983). Sexual selection functioning either through male-male competition or female choice is an essential ingredient of mating systems both at the time of pairing and later (Møller 1992). Behavioural observations of extra-pair copulations (Gladstone 1979; Birkhead and Møller 1992), DNA evidence of mixed paternity in apparently monogamous broods (Burke and Bruford 1987; Birkhead and Møller 1992) and the existence of a suite of morphological and behavioural adaptations (Harvey and Harcourt 1984; Birkhead and Møller 1992) have confirmed the importance of sperm competition (Parker 1970; Birkhead and Møller 1998) as a facet of sexual selection and mating systems.

The genetic outcome of a mating system is therefore determined by many factors. These include: (i) the observed pattern of social associations; (ii) the probabilities of females subsequently modifying their pairing decisions with extra-pair copulations (Kempenaers et al. 1992) and of males constraining them from doing so (Gowaty 1996; Birkhead and Møller 1996) - a battle fought with behavioural (Burke et al. 1989; Birkhead and Møller 1992; Wright 1998) and morphological adaptations (Birkhead and Møller 1992) within the constraints of the physical (e.g. preventing effective mate guarding) and social (e.g. increasing the availability of extra-pair males) environments; (iii) the occurrence of forced extra-pair copulations (McKinney et al. 1983); (iv) the occurrence of egg dumping (Brown 1984); (v) other factors which influence reproductive output (e.g. female allocation: (Cunningham 1997) or cryptic female choice (Eberhard 1996)).

2.1.2 Mating systems: cooperative breeding

In some species more than two adults provide parental care to offspring (Emlen 1984, 1991; Brown 1987; Stacey and Koenig 1990). A general consensus has been reached that the evolution of cooperative breeding is a two step process (Emlen 1982a,b, 1984, 1991; Brown 1987). First, an ecological constraint reduces the benefit of independent breeding relative to the benefit of philopatry causing adult offspring to remain at home (Koenig et al. 1991; Komdeur 1992). Second, either direct or indirect benefits accrue to individuals which help (Brown 1987; Emlen

1991; but see Jamieson and Craig 1987). Examples of direct benefits gained by helpers may include territory inheritance (Koenig and Stacey 1990; Wolfenden and Fitzpatrick 1990), breeding experience (Hatchwell et al. 1999) or reduced parental aggression (Clutton-Brock and Parker 1995). Helpers may also benefit indirectly as a result of increased inclusive fitness when by helping they increase the production of non-descendant kin (Emlen 1990).

2.1.3 Sociable weavers: social organisation and mating system

The social organisation of the sociable weaver has been described in considerable detail by Maclean (1973) who stressed its extreme coloniality and the intra-colonial organisation of birds into spatially defined social groups (nest masses). However, the reproductive behaviour of sociable weavers has only been patchily described (Maclean 1973; Collias and Collias 1978, 1980). For example, both Maclean (1973) and Collias and Collias (1978) report that socially monogamous pairs share the incubation, brooding and provisioning of offspring, but Maclean (1973) also includes anecdotal descriptions of multi-adult provisioning groups. This could indicate cooperative breeding (Brown 1987) or a complex mating system (Davies 1992). There have been no studies of the pattern of genetic outcome of the sociable weaver breeding system which, as copulations have rarely been observed (Maclean 1973, Collias and Collias 1978, Anderson 1995), is completely unknown.

2.2 AIMS

The central aim of this chapter is to describe the pattern of social behaviour associated with, and the genetic outcome of, the mating system of the sociable weaver in the context of its social organisation (i.e. coloniality). This includes three sub-aims:

(1) To corroborate and extend Maclean's (1973) observations on the importance of coloniality for social organisation in the sociable weaver. This includes the description of colony demography, patterns of individual space use within colonies and patterns of social behaviour.

(2) To corroborate and extend Maclean's (1973) and Collias and Collias' (1978) descriptions of the patterns of social interaction between breeding male and female sociable weavers and in particular to confirm the occurrence of cooperative breeding in the social weaver.

(3) To describe the genetic outcome of the mating system of the sociable weaver and to determine the rates of intraspecific brood parasitism and extra-pair paternity.

2.3 METHODS

2.3.1 Collection of field data

Adult birds were caught and processed (banded, measured, blood sample taken and parasite load assessed) as described in the general methods (chapter 1). The data presented in this chapter are primarily from the second and third field seasons (January 1997-June 1997 and November 1997-May 1998) as during the first field seasons many birds lost one or more colour bands (October 1995-April 1996) making identification difficult.

Weekly nest content checks were carried out as described in the general methods (chapter 1). Table 2.1 gives details of the colonies used in the study, the numbers of incubated clutches and the number of breeding groups at each colony.

Observational data were collected on the behaviour of marked birds during colony watches which lasted for three hours. Watches were divided into 18 sections (of ten minutes each) and mainly took place during the morning. During each ten minute section the identities of all birds present at the colony were recorded and observations of nest building, nest lining, provisioning, nest defence and aggressive behaviour (as defined by Collias and Collias 1978) were recorded for individuals on an *ad. lib.* basis. Particular emphasis was placed on provisioning behaviour and the identification of the chambers at which individuals were provisioning. The number of hours of observations at each colony are given in table 2.1. Collection of observational data was made difficult by the density of the nests, the downward orientation of chamber entrances, and problems in identifying and following individuals due to their fast flight patterns.

2.3.2 Molecular techniques

DNA was extracted from 456 blood samples using phenol-chloroform extraction (Bruford et al. 1992). Sex (Griffiths et al. 1998) and DNA microsatellite profiles were then determined using PCR amplification and silver staining.

(a) DNA extraction

DNA was isolated from the blood using a standard phenol-chloroform extraction protocol. A small sample of blood/tissue (1 µl) was placed to dry on a Kimwipe.

Table 2.1 (a). Summary of data collection (numbers of: incubated clutches; breeding groups; broods used for DNA analysis; broods with a known mother; and broods with all parents known) during the first field season (October 1995-April 1996). In the totals column, values with subscript a refer to additional clutches collected at other colonies. In the row reporting the number of clutches with identified parents, values without a subscript refer to the number of broods with parents confirmed by capture and provisioning records while values with subsript c record the number of cases in which the identity of adults was determined by capture alone. These clutches were not used in the analysis of provisioning behaviour.

Colony :	1	2	3	4	5	6	7	8	9	total
incub. clutches	2	29	3	3	1	3	7	3	9	60
breeding groups	2	22	3	2	1	3	5	3	7	48
DNA analysis	0	0	0	0	1	1	3	0	0	5, 1a
broods with mother	_	_	_	_	1	1	3	_	_	5, 1a
broods with adults	_	_	_	_	1c	1c	3c	_	_	5c, 1a

Table 2.1 (b) Summary of data collection (numbers of: incubated clutches; breeding groups; hours of behavioural observations; broods used for DNA analysis; broods with a known mother; and broods with all parents known) during the second field season (January 1997 - June 1997). In the hours of behavioural observations values with subscript v record the additionl hours of video footage. These data were not included in analyses. In the row reporting the number of clutches with identified parents, values without a subscript refer to the number of broods with parents confirmed by capture and provisioning records while values with subsript c record the number of cases in which the identity of adults was determined by capture alone. These clutches were not used in the analysis of provisioning behaviour.

Colony :	2	10	11	15	17	20	21	22	total
incub. clutches	21	14	8	16	5	8	2	1	75
breeding groups	10	6	4	6	3	6	2	1	38
hours obs.	40, 12v	-	16, 3v	9, 3v	-	4	-	-	69, 18v
DNA analysis	19	10	5	5	-	3	1	0	43
broods with mother	13	2	1	1	_	2	_	_	19
broods with adults	10 (2c)	_	1 (1c)	1	_	2	_	_	14 (3c)

Table 2.1 (c) Summary of data collection (numbers of: incubated clutches; breeding groups; hours of behavioural observations; broods used for DNA analysis; broods with a known mother; and broods with all parents known) during the third field season (November 1997 - May 1998). In the totals column, the value with subscript a refers to the number of additional clutches collected at other colonies. In the row reporting the number of clutches with identified parents, the top value is the total number, the lower number (subsript c) is the number of cases in which the identity of those adults was determined by capture. These clutches were not used in the analysis of provisioning behaviour.

Colony :	2	10	11	12	23	24	25	27	28	29	30	31	32	33	34	35	total
incub. clutches	7	4	2	3	3	1	4	9	5	4	1	8	5	2	3	4	65
breeding groups	7	3	2	2	3	1	4	8	4	2	1	8	5	3	3	3	59
hours obs.	39	21	24	6	18	6	15	0	0	12	0	9	15	3	3	3	174
DNA analysis	5	3	2	2	2	-	2	-	-	2	-	8	2	1	-	1	30
broods with mother	4	2	2	_	2	_	2	_	_	1	_	2	2	_	_	_	17 (4a)
broods with adults	4	2	2 (1c)	_	2	_	2	_	_	1	_	_	_	_	_	_	13 (1c)

The dry sample was then placed in a screw top eppendorff tube containing 500 µl of 1mM Tris HCl, pH 8.0; 0.1M NaCl; 1mM EDTA; 0.5% SDS. Five units of proteinase K (Sigma) were then added. Samples were incubated overnight (37°C) in a turning oven. In order to extract DNA from these samples 500µl of phenol/chloroform mixture (25 parts phenol: 24 parts chloroform: 1 part iso-amyl alcohol) was added to each eppendorff. After mixing by shaking the eppendorffs were centrifuged (15,000 revs/min for 10 mins). The supernatant was removed using a Gilson pipette and transferred to a new eppendorff. This procedure was repeated once with phenol/chloroform (as before) and once with choloroform (24 parts chloroform: 1 part iso-amyl alcohol). DNA was precipitated from the resultant supernatant using two volumes of 100% ethanol followed by two volumes of 70% ethanol. The resulting DNA pellets were air dried overnight then dissolved overnight (4°C) in 500µl of ultra pure water. Samples were stored at -20°C.

(b) Sex determination

Sex determination was carried out using the method of Griffiths et al. (1998) which takes advantage of the possession of the W sex chromosome in female (ZW) but not male (ZZ) birds. Griffiths et al. (1998) have developed two primers (P2 and P8) which anneal to conserved exonic regions of the CHD-W (an avian W chromosome gene) and CHD-Z (a related gene found on the Z chromosome) genes. As these primers amplify across an intron in both genes, and the length of the intron differs between the CHD-W and CHD-Z, the sexing of birds is simple; gel electrophoresis reveals one band in males but two in females.

PCRs were carried out in 15µl reactions in a Hybaid 'Touchdown' Thermal cycler. The final reaction mixture contained 0.5 units of *Taq* 'Thermoprime plus' DNA polymerase (Advanced Biotechnologies), 1.5 µM of each primer, 0.2 mM DNTPs, 2.5mM $MgCl_2$, 20mM $(NH_4)_2SO_4$, 75mM Tris-HCL pH 8.8, 0.15mg/ml DNAse fee BSA, 0.7µl/ml ß-mercaptoethanol and 50 to 100 ng of template DNA. The PCR conditions used were an initial denaturing step of 94°C for 1min 30 seconds followed by 40 cycles of 50°C for 20s, 72°C for 25s and 94°C for 15s.

Products were separated by electrophoresis on a 3% agarose gel (250 ml ultra-pure water; 7.5g agarose; 11.5µl of ethidium bromide) run at 100V for 90 minutes. To test the accuracy of the method sixteen samples from birds of known sex were tested (nine males and seven females); the sexes of all of these samples were correctly assigned.

(c) PCR amplification

Four primer pairs (Pdo 1, Pdo 3 and Pdo 4 (Neumann and Wetton 1996) and Pdo 5 (Griffith 1998)) were used in this study. The genotype of each individual was determined using PCR amplification. The products were electrophoresed on polyacrylamide gels, which were then silver stained.

PCRs were carried out in 10 µl reactions in a Hybaid 'Touchdown' Thermal cycler. Each 10µl reaction mixture contained 0.25 units of *Taq* 'Thermoprime plus' DNA polymerase (Advanced Biotechnologies), 1.5 µM of each primer, 1.0 mM (for Pdo1 and Pdo4) or 1.5 mM $MgCl_2$ (for Pdo3 and Pdo5), and 0.2 mM dNTPs in the manufacturers buffer (Buffer IV, Advanced Biotechnologies). 50-100 ng of template DNA was used. Each PCR started with an initial denaturing step of 94°C for 120s this was followed by 35 cycles of 30s at the annealing temperature, 60s at 72°C, 15s at 94°C. The annealing temperatures were 59°C for Pdo1, 54°C for Pdo3 and Pdo5 and 57°C for Pdo4. The PCR products were stored at -20°C until they could be electrophoresed.

The samples were electrophoresed in denaturing 6% polyacrylamide gel (Accugel sequencing grade, National diagnostics). A 50 base pair ladder was run after every 12 samples to aid determination of allele sizes. Gels were run at 60W (temperature approximately 50°C). Pdo4 and Pdo5 products were run for around three hours, Pdo1 and Pdo3 for around 2 hours. Gels were fixed in 10% glacial acetic acid for 20 mins. After washing with ultra-pure water (three times) they were stained for 30 mins in 200ml of a 0.1% w/v silver nitrate solution containing 300µl of 37% formaldehyde. After briefly rinsing the gel was developed in 200ml of chilled 0.3M sodium carbonate solution containing 300µl of 37% formaldehyde and 40µl of 10% sodium thiosulphate. The reaction was halted, once the bands were visible, using 10% acetic acid. The gel was then rinsed and allowed to dry, before it was scored and photographed.

2.3.3 Data analysis

(a) Social organisation and social behaviour

In order to describe the dispersion of individuals, ringing and sexing data were used to calculate the size and sex ratios of the study colonies. The frequencies of male and female presence (proportion of ten minute sections), and rates of nest building, aggressive behaviour and rosy-faced lovebird *Agapornis roseicollis* mobbing were calculated (See Table 2.1 for details of hours of observations; lovebird mobbing data were collected only in 1998). Responses to rosy faced

lovebirds were used as a measure of nest defense activity as the lovebirds frequently prospected sociable weaver colonies looking for potential nesting chambers and during these visits sociable weavers responded with intense mobbing behaviour. In order to test Maclean's (1973) assertion that birds are restricted to certain nest masses the proportion of time which different individuals spent at each of the two nest masses (B and C) at Colony 2 was determined.

(b) Mating systems: social associations

As both pairs (two adults) and trios (three adults) were recorded provisioning offspring, reproductive units were described as groups. While it was not difficult to follow the laying patterns of groups (from the nest chamber used and the appearance of the eggs) it was difficult to determine their exact membership. Provisioning observations and/or captures of individuals in their chambers at night were used to identify the social parents of offspring (Table 2.1). If one or more provisioning adults were unidentified or uncertain the brood was excluded from further analyses. Of the 27 broods with confidently identified parents: for 20 broods all group members were determined on the basis of provisioning observations; for two broods group membership was determined on the basis of provisioning for the male(s) and capture for the female; and for five broods group memberships were determined on the basis of captures alone (totals: 14 broods from 1997 and 13 from 1998). Thus the sample sizes for the analysis of social mating systems and genetic outcomes were small.

Provisioning data (n = 16 groups (21 broods) with all adult provisioning rates: 7 trios, 9 pairs) collected as close as possible to chick age 14 days (means: pairs = 12 days, trios = 16 days) were used for comparison of total provisioning rates. To avoid pseudoreplication, when data was collected from more than one brood per group, only data from the earliest brood was used.

In order to compare the provisioning rates of males and females paired tests were used within groups. For pairs, both male and female feeding rates were recorded for nine groups (male but not female rate was also recorded for one group). For trios, the provisioning rate of the male gaining paternity (Section 2.4.3) was compared against that of the other male and the female. There were seven trios with provisioning data for both males and the female and one trio with data for both males but not the female. Thus, for trios, the two males could be compared in eight cases and each of the males with the female in seven cases.

To investigate the effect of social mating system on reproductive success, group means for clutch size, hatchlings per clutch, fledglings per clutch (calculated over all attempts in a breeding season) and the total number of clutches incubated and the total number of fledglings produced over the breeding season (Davies 1992) were used. As the data set is very small (n = 20 groups split between two years) the data from the two years were analysed together with year as a factor.

(c) Mating systems: genetic outcomes

Determination of paternity was carried out by exclusion using 33 clutches with known social parents (6 from 1996 (not included in provisioning analysis), 14 from 1997 and 13 from 1998). For an additional 14 clutches only the social mother was known and these clutches were included in the analysis of frequency of egg dumping. Only three loci (Pdo1, Pdo3 and Pdo5) were used in the initial exclusions as Pdo4 was highly variable and difficult to score repeatably. However, Pdo4 was used to validate exclusions based on the other three loci when there was a considerable size difference between parental and offspring alleles at Pdo4. Data on the available loci, calculated using Cervus (Marshall et al. 1998), are reported in Table 2.2.

2.4 RESULTS

2.4.1 Social organisation

(a) Colony size and sex ratios

Adult population size at the colonies used for the collection of behavioural observations varied between four and 30 birds (mean = 14.4, median = 14, n = 13: 4 colonies used in both 1997 and 1998, 8 colonies used in 1998 only). In 1997 the mean adult sex ratio (males: females) at a colony was 1.55 (± 0.20, n = 5 colonies). In 1998 the adult mean sex ratio at a colony was 1.08 (± 0.07, n = 8 colonies). However, when individuals from all colonies were combined, there was no significant difference between years (1997: males = 53, females = 35, 1998: males = 69, females = 62; chi^2 = 1.21, df = 1, NS). Nor was there a significant difference from a one:one ratio within either year (1997: males = 53, females = 35: chi^2 = 3.68, df = 1, $0.1 > p > 0.05$; 1998: males = 69, females = 62: chi^2 = 0.37, df = 1, NS).

(b) Social behaviour

On average each bird was observed at the colony during 22% (n = 144 birds, 8 colonies) of ten minute colony watches. However, males were observed at the colony significantly more frequently than females (Median proportion of watches

Table 2.2: Microsatellite primers and variability details; indicating the nature of the repeat sequence, the number of alleles found (N_A), the observed (H_O) and expected (H_E) heterozygosity for each allele (expected values calculated with CERVUS (Marshall et al. 1998)), and the average probability of exclusion for first (P_{E1}) and second (P_{E2}) parents (the average probability of excluding a randomly chosen individual from parentage of an offspring with (P_{E2}) or without (P_{E1}) genetic information from the other parent calculated using CERVUS (Marshall et al. 1998).

Locus	Reference	Repeat	N_A	H_O	H_E	P_{E1}	P_{E2}
Pdo1	Neumann and Wetton (1996)	$(TG)_n$	4	0.200	0.211	0.023	0.109
Pdo3	Neumann and Wetton (1996)	$(TCCA)_n$	18	0.800	0.887	0.629	0.773
Pdo5	Griffith (1998)	$(CA)_n$	26	0.819	0.900	0.665	0.799
Combined	-	-	-	-	-	**0.879**	**0.959**

present: males = 0.22, n = 82; females = 0.11, n = 56; Mann-Whitney: W = 6236.5, p(corrected for ties) = 0.02). On average 71% (n = 8 colonies; min = 46% (n = 15 birds), max = 100% (n= 4 birds)) of birds were observed to build the communal nest but this may be an underestimate as the proportion of birds observed building increased with per capita observation time (r_s = 0.70, n = 9, p < 0.02).

The rate of nest building was significantly greater for males than females (males: median = 0.14 (mean = 0.29) builds/hr, n = 82; females: median = 0.04 (mean = 0.11) builds/hr, n =56; Mann-Whitney: W = 6360, p(corrected for ties) = 0.004). Additionally, males were observed acting aggressively (males: median = 0.02 (mean = 0.06) aggressive interactions/hr, n = 82 birds; females: median = 0.00 (mean = 0.01) aggressive interactions/hr, n = 56; Mann-Whitney: W = 6483, p(corrected for ties) = 0.0001) and mobbing lovebirds (1998 data only; males: median = 0.00 (mean = 0.05) mobbings/hr, n = 50 birds; females: median = 0.00 (mean = 0.01) mobbings/hr, n = 39; Mann-Whitney: W = 2521, p(corrected for ties) = 0.003) more frequently than females.

Thus, sociable weavers spend around one fifth of their time at the colony on average and almost three quarters of birds are observed adding to it. However, there are significant behavioural differences between male and female sociable weavers; males built the nest, acted aggressively and mobbed lovebirds more frequently than females. Within the sexes there were large differences between mean and median rates of behaviour suggesting considerable variation between individuals.

(c) Nest mass use

Individuals at colony 2 did not divide their time equally between the two active nest masses; several individuals were observed only at nest mass C while others were generally seen at nest mass B (Figure 2.1). Furthermore, for birds present in both 1997 and 1998 there was a significant correlation between the proportion of time spent at nest mass C in 1997 and 1998 (r_s = 0.96, n = 15, p < 0.001). Thus, at colony 2, sociable weavers showed fidelity to a particular nest mass.

2.4.2 Mating system: social associations

(a) Occurrence of pairs and trios

During the 1997 breeding season the identities of all birds provisioning at 14 of a total of 75 clutches (9 of 38 independent breeding groups) were determined from capture records and behavioural observations. Seven (50%) clutches were

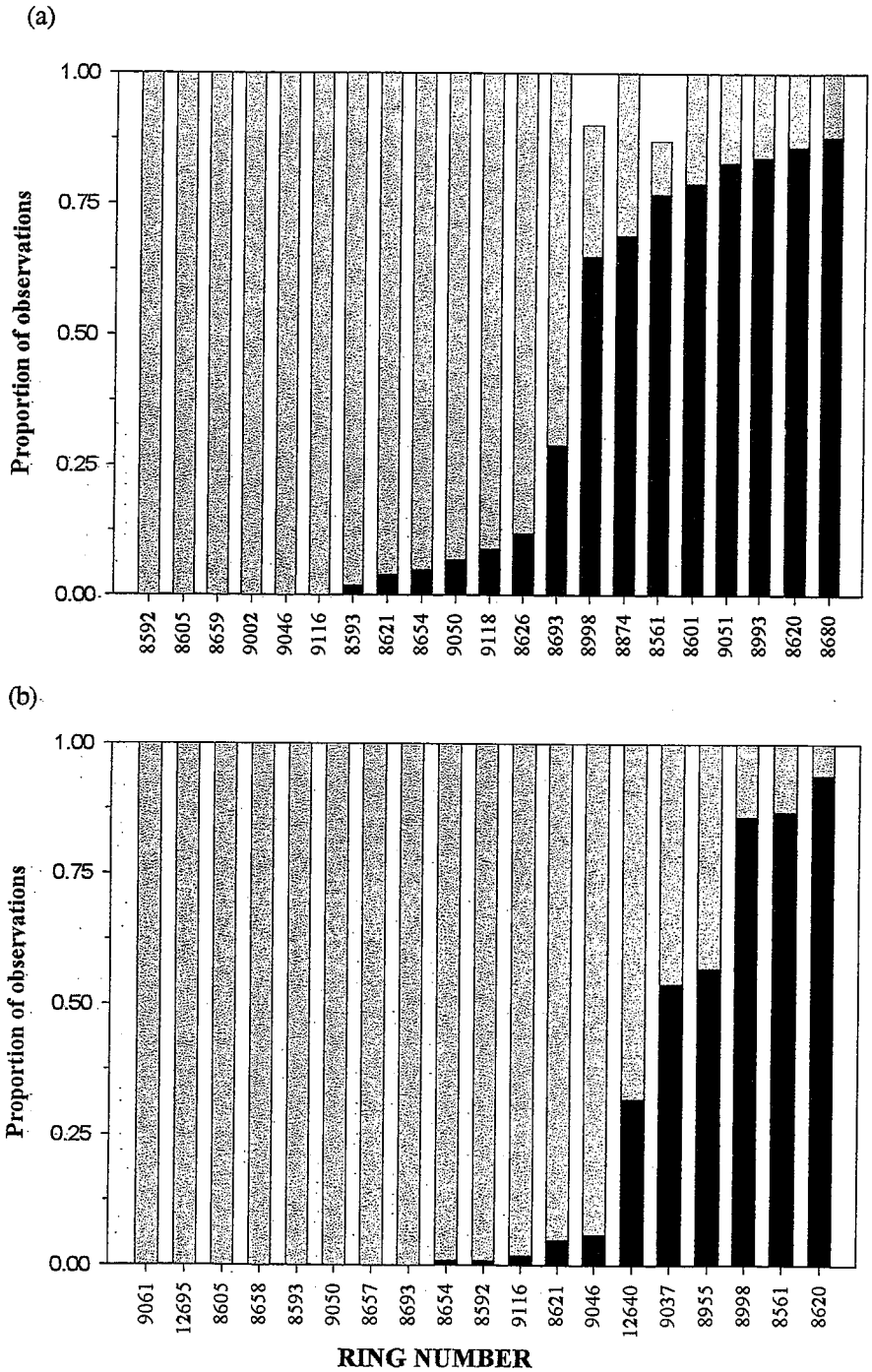


Figure 2.1. Proportion of observations of individual birds at nest masses B (black) and C (grey) of colony 2 during the (a) 1997 and (b) 1998 field seasons. Only birds for which position was recorded at least 10 times are included. Mean number of location records in 1997 was 30 (min 11, max 64) and in 1998 was 64 (min 13, max 140).

provisioned by three adults (5 out of 9 breeding groups). The remaining 7 clutches were provisioned by a pair of adults (4 out of 9 breeding groups). During the 1998 breeding season the identities of all birds provisioning at 13 out of a total 65 clutches (11 of 59 independent breeding groups) were determined. Three adults were provisioning the offspring in five (38%) clutches (4 out of 11 breeding groups). At the remaining 8 clutches (7 out of 11 breeding groups) provisioning was by a pair. On the basis of these data it appears that around half of breeding groups are composed of three adults and the half are pairs.

(b) Patterns of trio membership

In all groups of three birds (trios), two birds were males and one female. Unfortunately, little was known about the pedigree or history of group members; although in one case (in 1998) a son (ringed as a chick in 1997) was helping to provision his mother's offspring. Insufficient microsatellite data were available to allow the calculation of accurate estimates of pairwise relatedness between group members.

(c) Provisioning behaviour

The total provisioning rate at a chamber (male(s) plus female) was not significantly influenced by year, chick age or number of adults provisioning (GLM $\sqrt{(x + 0.5)}$ transformed data: Factor year, $F_{1,14} = 1.78$, $p = 0.20$; Factor chick age, $F_{1,14} = 0.01$, $p = 0.91$; Factor number of adults, $F_{1,14} = 0.01$, $p = 0.93$). However, the number of chicks present had a significant effect on the total feeding rate (GLM $\sqrt{(x + 0.5)}$ transformed data: Factor number of chicks, $F_{3,14} = 5.09$, $p = 0.01$).

As observations for males and females provisioning together were matched, paired tests were used to compare male and female feeding rates. For birds breeding in pairs there was no significant difference between mean male (1.62 ± 0.47, $n = 10$) and female (2.03 ± 0.48, $n = 9$) feeding rates (Figure 2.2.a; paired Wilcoxon signed rank test: $W = 29$, $n = 9$, $p = 0.48$). For birds breeding in trios, the average male feeding rate (over the two males: 0.85 ± 0.19, $n = 8$ groups) was lower than the average female feeding rate (1.46 ± 0.51, $n = 7$). This difference was not significant (paired Wilcoxon signed rank test: $W = 23$, $n = 7$, $p = 0.15$).

(d) Reproductive effort and success in pairs and trios

Group type had no significant effect on five measures of reproductive effort and/or success (mean clutch size, mean hatchlings per clutch, mean fledglings per clutch, total clutches incubated and total fledglings: Fig 2.3; Table 2.3).

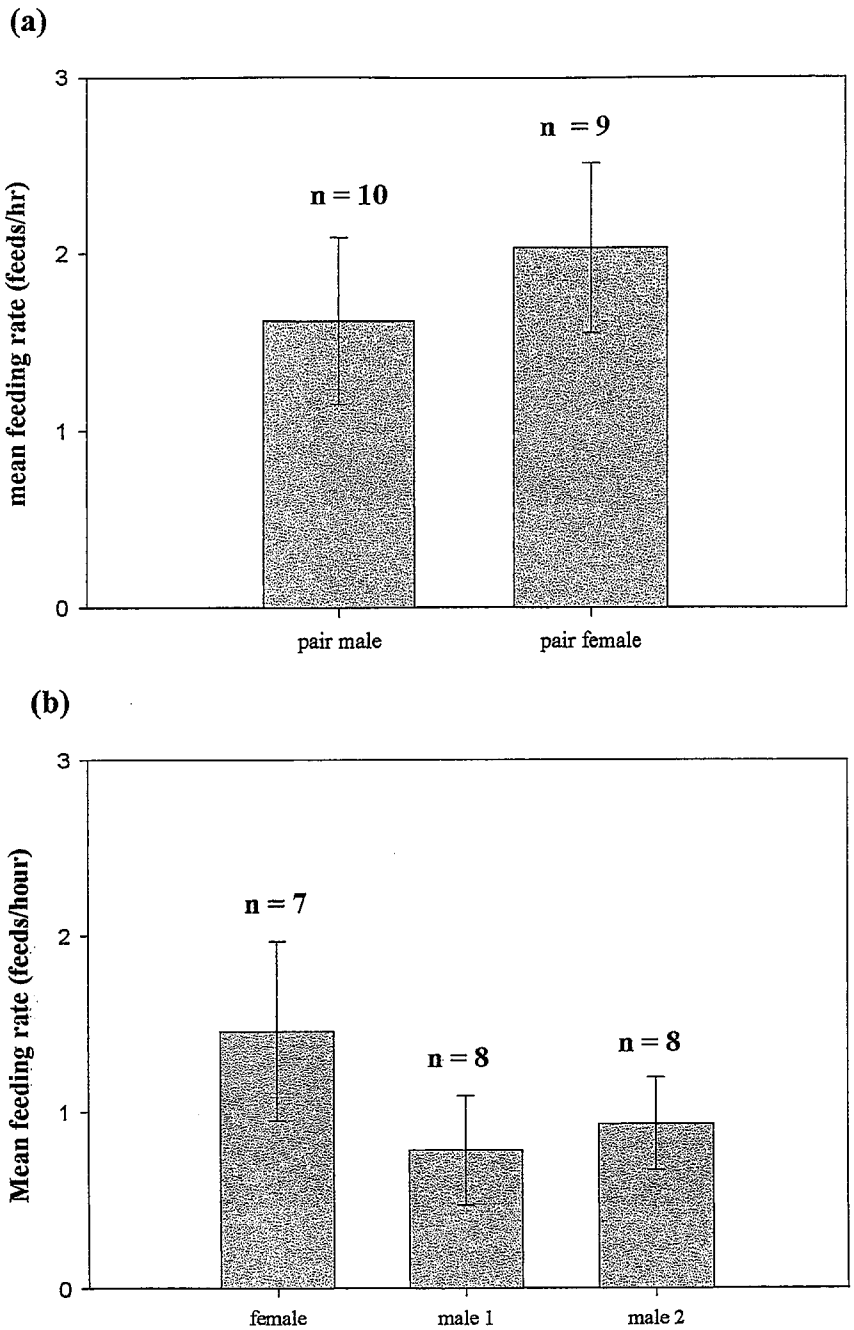


Figure 2.2 Frequency of provisioning within breeding groups:
(a) Within pairs there was no significant difference in provisioning rate between males and females (Wilcoxon signed rank test: W = 29.0, n = 9, p = 0.477).
(b) Within trios there was no significant difference in provisioning rate between the two males (Wilcoxon signed rank test: W = 8.0, n = 8, p = 0.353). Both males fed less frequently than the female however only the difference between the male with paternity (male 1) and the female approached significance (male 1 v female, Wilcoxon signed rank test: W = 15, n = 7, p = 0.059; male 2 v female, Wilcoxon signed rank test: W = 19, n = 7, p = 0.447).

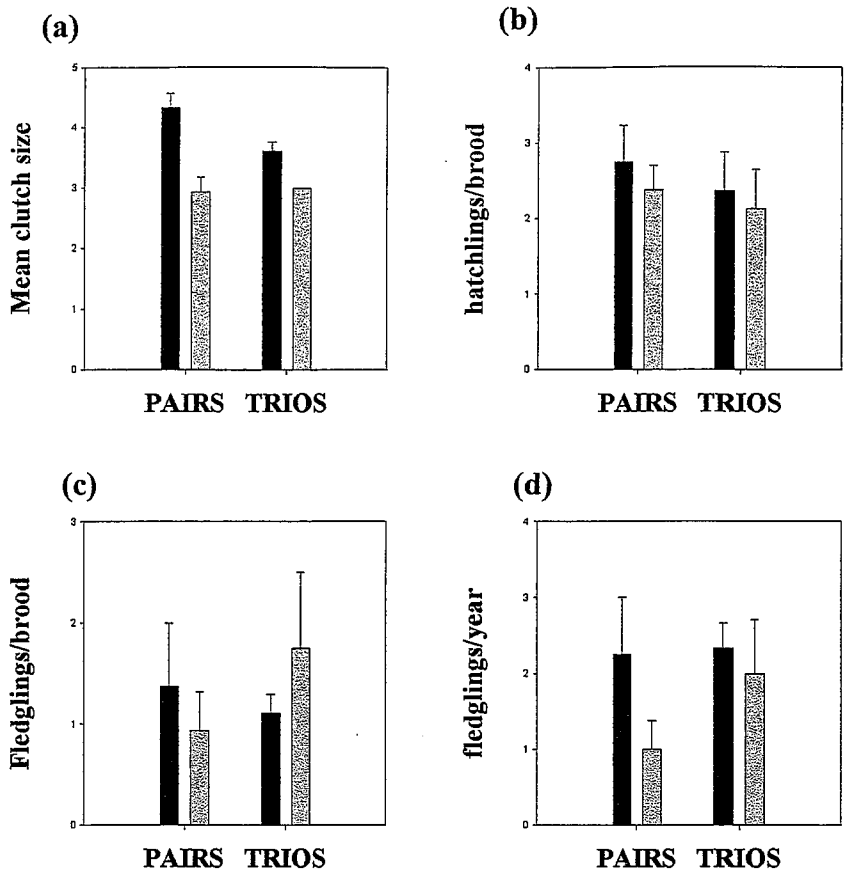


Figure 2.3 Reproductive success in pairs and trios. Data are for 4 pairs and 5 trios in 1997 (black) and 7 pairs and 4 trios in 1998 (grey). There were no significant differences in (a) clutch size, (b) hatchlings/brood, (c) fledglings/brood or (d) total fledglings/year (Table 2.3).

Table 2.3: The role of group type (pair or trio), year (1997 or 1998) and the interaction term in explaining variation in five measures of reproductive effort/success in the sociable weaver. Clutch size, hatchlings and fledglings (measures i, ii and iii) were calculated as the mean of all breeding attempts by a group in a year. Totals (measures iv and v) were calculate as the total number of clutches incubated and chicks fledged over a breeding season. Analysis was carried out using GLM. There were no significant effects of group type. In all cases df = 1,17.

Reproductive parameter	Factor: Type of group	Factor: Year	Interaction: year*(group type)
Mean clutch size	F = 2.02; NS	F = 17.90; p = 0.001	F = 2.85; NS
Mean hatchlings	F = 0.12; NS	F = 1.15; NS	F = 0.05; NS
Mean fledglings	F = 0.41; NS	F = 0.01; NS	F = 0.98; NS
Total clutches incubated	F = 0.26; NS	F = 6.44; p = 0.021	F = 0.26; NS
Total fledglings	F =1.14; NS	F = 2.34; NS	F = 0.62; NS

2.4.3 Mating systems: genetic outcomes

(a) Division of paternity between males within trios

Microsatellite profiles were determined for offspring provisioned by trios (n = 12 groups with 15 broods: 7 from 1997, 5 from 1998 and 3 from 1996). All broods provisioned by each group were combined. Paternity could be determined for two or more intra-group chicks (i.e. one of the males had paternity) for nine groups (one group had only intra-group chick, and for two groups either male could have fathered one or more of the chicks). In all of these nine groups only one male gained paternity paternity ($p < 0.002$, assuming equal fertilizing probability).

There was no difference in provisioning rate between the two males (Fig 2.2.b; paired Wilcoxon signed rank test: W = 8, n = 6, p = 0.35). However, both fed less frequently than the female, although not significantly so (Fig 2.2.b; male gaining paternity v. female, paired Wilcoxon signed rank test: W = 15, n = 7, p = 0.059; male without paternity v. female, paired Wilcoxon signed rank test: W = 19, n = 7; p = 0.45).

b. Occurrence of brood parasitism

For six out of 101 chicks (6%) the social mother was excluded from maternity based on comparison of the DNA profiles of the social parents and the offspring. In four cases this was based upon a mismatch at one locus and in two cases upon mismatches at two loci. These six chicks came from five clutches; brood parasitism occurred in 11% of clutches (5 out of 47).

c. Occurrence of extra-group paternity

For the 70 chicks with known social parents the social father was excluded as a genetic parent on the basis of microsatellite profiles in 11 cases (17%). In eight cases there was a mismatch at one locus and in three cases mismatches at two loci. The eleven extra-group chicks came from nine clutches; extra-group paternity therefore occurred in 27% of clutches (9 out of 33).

There was no difference in the frequency of clutches containing extra-group young between pairs and trios (pairs: 6 out of 18 clutches; trios 4 out of 15; $Chi^2 = 0.17$, df = 1, NS). Nor was there a difference in the frequency of extra-group offspring between pairs and trios (pairs: 6 out of 34 chicks, trios 5 out of 36 chicks; $Chi^2 = 0.19$, df = 1, NS).

2.5 DISCUSSION

Five main results are presented in this chapter. (1) There were significant differences in social behaviour between male and female sociable weavers. Males spent more time at colonies than females. They also built the communal nest, were aggressive and mobbed lovebirds more frequently. (2) There was some evidence of socio-spatial division within colonies. At colony 2 individuals were not sighted equally frequently on each of two nest masses. (3) Approximately 45% of female sociable weavers breeding at the study site were aided in provisioning their young by two males. The remaining 55% of females bred in pairs. It was not possible to determine the genetic relatedness between the three birds in trios. (4) For every brood (for which genetic paternity was determined) fed by two males only one male gained paternity of within group offspring. (5) Both intraspecific brood parasitism (6% of chicks) and extra-group paternity (17% of chicks) occurred. There was no difference in the frequency of extra-group paternity between pairs and trios.

2.5.1 Social organisation of the sociable weaver

Colonies form a focus for social behaviours in the sociable weaver with the average bird spending around twenty percent of its time at the colony. Sociable weavers add to the nest mass frequently (although this is split between additions to their own nest and general building (Collias and Collias 1978)), form groups mobbing lovebirds and leave the colony together in large feeding flocks (Maclean 1973; pers. obs.). Differences in behaviour both between and within sexes are suggestive of the dominance described by Collias and Collias (1978), who found that while most male sociable weavers are dominant over females, some males are highly subordinate, rarely nest build and do not pair. Maclean (1973) also observed differences in dominance, reporting that while most birds remain on their own nest mass, a few highly aggressive individuals visit all nest masses at a colony. Unfortunately, in the present study collecting data on wild birds proved difficult so detail was limited compared with Collias and Collias' (1978) aviary study of ten birds.

The evidence of individual differences in nest mass use corroborated Maclean's (1973) findings. However the sociable weaver social system does not rigidly divide birds into discrete colonies. Individuals from different colonies did meet, either when foraging (e.g. during November/December 1995 ringed individuals from colony two were observed foraging with many unringed birds) or when they visited colonies other than their own. Some of these visitors were day trippers (4

birds roosting at colony 11 frequently visited colony 23 during March 1998; see Fig 1.5). In other cases they initiated breeding attempts at a colony near their own (in 1997 two pairs from colony 20 initiated clutches at colony 21 and in 1998 two pairs from colony 11 initiated clutches at colony 23; see Fig 1.5). Taken together these observations suggest that the patterns of spatial and social delimitation in the sociable weaver may be complex, but that individuals are almost certainly not limited to interactions within their own colony.

2.5.2 Mating systems: social associations and genetic outcomes

(a) Cooperative breeding

Slightly under half of sociable weaver females laid clutches which were provisioned by two males. There was no sharing of paternity between the two males suggesting cooperative breeding (Emlen 1991) rather than cooperative polyandry (Davies 1991; Hartley and Davies 1994; Winterbottom et al. 1999). This confirms Maclean's (1973) report of occasional helping and is consistent with the occurrence of cooperative breeding in the closely related white browed sparrow weaver *Plocepasser mahali* (Lewis 1982) and grey capped social weaver *Pseudonigrita arnaudi* (Collias 1984; Bennun 1989, 1992, 1994).

A detailed investigation of the benefits of helping in the sociable weaver was not attempted during the present study. However, when there are non-breeding adults available to help in a population, two types of factors are believed to be of importance in explaining the evolution of helping behaviour (Brown 1987; Emlen 1991): (i) the direct consequences of helping for helpers (e.g. acquisition of territory (Wolfenden and Fitzpatrick 1990), skills (Hatchwell et al. 1999) or mates (Reyer 1990) or reduced parental aggression (Clutton-Brock and Parker 1995); (ii) the indirect consequences of helping for helpers. The indirect consequences are determined by the increase in LRS of the breeder as a result of helping and the relatedness between the helper and the breeders offspring (Hamilton 1964a,b; Brown 1987; Emlen 1991).

During the present study it was impossible to determine the pattern of relatedness between helpers and breeders due to: (i) limited genealogical information; and (ii) insufficient microsatellite data to accurately determine pairwise molecular estimates of kinship (Queller and Goodnight 1989; chapter 5). However, some (albeit sparse) data were collected on provisioning and reproductive success in pairs and trios.

Neither total provisioning rate nor reproductive success (measured as total fledglings over the breeding season) varied significantly with presence of a helper. However these comparisons are not necessarily meaningful, for example if, as Emlen (1990) suggests, helping is more likely in poor conditions (and indeed Figure 2.3 suggests a slight (non-significant) increase in reproductive success in trios compared to pairs in year three but not year two). Much more information is needed to investigate such trends. Male feeding rate was almost significantly lower than female feeding rate in trios but not pairs. This did not appear to result from lower confidence of paternity as the frequency of extra-group paternity did not vary between trios and pairs (Davies 1991; Mulder et al. 1994; Wright 1998). However, reduced provisioning rate may equate with increased survival - a potential indirect benefit if helpers and breeding males are related.

Clearly more research is needed to develop an understanding of the factors selecting for helping in the sociable weaver. Such research would need to both confirm and extend the findings of the current study, with particular emphasis on: (i) the frequency of helping and the conditions favouring its occurrence (Emlen 1990; Du Plessis et al. 1995); (ii) the pattern of helping - which birds help (i.e. do helpers help their relatives?) and when do they help (do helpers attempt to breed first? (Emlen 1990)); (iii) the response of breeders to helper provisioning rate; (iv) the consequences of being helped for breeders - reproductive success and survival; (v) the long term consequences of helping for helpers.

(b) Extra-pair paternity

The frequency of extra-pair paternity reported in this chapter falls near to the centre of the range found in passerines (Birkhead and Møller 1995; Stewart 1999). And interestingly, while the relatively large testes mass of male sociable weavers (Winterbottom 1997) is consistent with the occurrence of frequent extra-pair paternity (Møller and Briskie 1995), the lack of sexual dimorphism (Møller and Birkhead 1994) is not. The relationship between colony size and extra-group paternity is investigated in chapter 3. As extra-pair male identities could not be assigned and the availability of behavioural data was limited, it is difficult to comment upon the detail of the extra-pair mating system in the sociable weaver. Only one copulation was observed during this study. It occurred at some distance (approximately 200m) from colony 3 between two members of a small group, which had recently left the colony. The departure of such groups from colonies is common (pers. obs.) and if as Anderson (1995) has suggested, extra-pair copulations occur away from the colony, the departure of these groups may be related to the occurrence of extra-pair copulations. Another interesting possibility is

that day tripping between colonies could lead to extra-colony paternity. This has implications for patterns of gene flow (Chapter 5).

(c) Intraspecific brood parasitism

By dumping eggs in the nests of other birds females can increase their reproductive success without paying the costs associated with raising offspring (Yom-Tov 1980). In this study eleven percent of clutches included dumped eggs producing six percent brood parasite young over all. The rates of intraspecific brood parasitism (IBP) vary considerably between species. While some studies report frequent IBP (cliff swallow *Hirundo pyrrhonata* at least 22% and possibly 43% of nests (Brown and Brown 1989 but for a molecular assessment see Smyth et al. 1993); purple martin *Progne subis* 36% of nests (Morton et al. 1990); zebra finch *Taeniopygia guttata* 36% of nests (Birkhead et al. 1990); sand martin *Riparia riparia* 9% of nests (Alves and Bryant 1998)) many report no parasitism (reviewed in Hartley et al. 1993). So the frequency of intra-specific brood parasitism recorded in sociable weavers represents the low end of the continuum for species in which egg dumping does occur. As eggs experimentally added to sociable weaver clutches after the start of incubation are not removed (pers. obs.) the variation in egg pattern between individuals does not seem to aid identification and ejection of parasitic additions. However, it is possible that continuous incubation (Maclean 1973) represents a defence against brood parasitism in the sociable weaver.

2.5.3 Potential sources of error in paternity analysis

(a) Behavioural data

Collecting data on sociable weaver behaviour is made difficult by the close positioning of nest chambers, the density of birds and their speed of movement around the colony. As confidence in the pattern of social association is an essential prerequisite for a meaningful analysis of the pattern of genetic outcome of a mating system, this made the determination of the frequencies of egg dumping and extra-group paternity surprisingly difficult. In order to minimise error only clutches for which definite social parents had been identified were used.

(b) Molecular techniques

Mistakes may occur during the determination of paternity as a result of experimental error, or the occurrence of null alleles or mutations (Pemberton et al. 1995; Neumann and Wetton 1996). While Pdo1 and Pdo3 were easy to score, Pdo4 and Pdo5 were difficult unless parents and offspring were adjacent on a gel. Thus, to minimise the possibility of false exclusion Pdo 4, which also has a high mutation rate (Neumann and Wetton 1996), was not used in the final analysis and

mismatches at Pdo5 were only accepted as mismatches when parental and offspring allele size differed by at least 6 base-pairs (Pdo5 has a 2 bp repeat). As the probability of exclusion was only 0.959 for the second parent (using Pdo1, Pdo3 and Pdo5) the cut off level for rejection of paternity was set as one mismatch. A higher level might have dramatically increased the probability of type II errors; the false inclusion of social parents.

Additionally, coloniality and low dispersal may create high local relatedness in the sociable weaver (Chapter 5). If potential fathers are related the actual probability of exclusion will be lower than the mean pan-sample value (Girman et al. 1997; Marshall et al. 1998). This creates two problems: (i) If paternity is lost to relatives social fathers may not be excluded even when not the genetic father (type II error). (ii) In conjunction with the relatively low number of loci used it meant that the assignment of extra-pair paternity to particular males could not be meaningfully attempted.

2.5.4 Conclusions

Sociable weavers have a complex mating system which includes facultative cooperative breeding. In order to investigate the form of cooperation in the sociable weaver, further studies producing larger data sets are needed. Both extra-group paternity and intra specific brood parasitism occur at moderate levels in the sociable weaver.

CHAPTER 3: MAINTENANCE OF COLONIALITY

3.1 INTRODUCTION

Despite the importance of coloniality for many aspects of a species' ecology, no consensus has been reached on the factors selecting for the evolution of colonial living (Birkhead 1985; Wittenberger and Hunt 1985; Siegel-Causey and Kharitonov 1990; Danchin and Wagner 1997). This is partly because, once coloniality has evolved, it may influence many aspects of a species' social environment leading to further adaptations and thus confounding cause and consequence (Siegel-Causey and Kharitonov 1990). However, while explanation of the evolution of coloniality is difficult it may be possible to gain understanding of the factors which influence its maintenance (Brown and Brown 1996).

3.1.1 Equilibrium approach: costs and benefits of coloniality

The equilibrium (or cost/benefit) approach to coloniality is based upon the assumption that individuals breed in colonies when the benefits outweigh the costs (Alexander 1974). Thus, if the costs and benefits of colonial living can be determined it may be possible to explain why coloniality is maintained. Although measuring the costs and benefits of colonial versus solitary living is difficult the qualitative effects of natural variation in colony size for determinants of individual fitness may provide reasonable indications (Hoogland and Sherman 1976; Møller 1987; Brown and Brown 1996). There are at least three potential problems with the equilibrium approach: (i) some costs or benefits are inherent in coloniality and may not vary with colony size; (ii) individuals may assort non-randomly between colonies so that variation in colony size is confounded by variation in individual quality (Møller 1987; Brown and Brown 1996); and (iii) no unifying currency is available to measure the costs and benefits (Birkhead 1985).

Although much research has focused on the ultimate costs and benefits relating to survival and natural resource availability (Vessems and Draulans 1986) the costs and benefits of alternative reproductive strategies at colonies have also attracted interest (Møller 1987; Morton et al. 1990; Birkhead and Møller 1992).

3.1.2 Costs of coloniality

The potential costs of coloniality are obvious and manifold. First, if resources are limited then as the number of individuals depending on them increases the per capita availability decreases. In colonies competition for valuable resources, such as food

or nest sites, will be greater leading to a reduced chance and increased cost of obtaining sufficient resources (Alexander 1974; Hoogland and Sherman 1976; Hunt et al. 1986; Wiklund and Andersson 1994). Second, the transmission of parasites and pathogens may be facilitated in colonies (Alexander 1974; Hoogland and Sherman 1976; Brown and Brown 1996). Third, colonies could lead to increased predator attraction (Wittenberger and Hunt 1985; Brown and Brown 1996). Fourth, costly behavioural interactions may become more common (e.g. infanticide (Wittenberger and Hunt 1985; Møller 1987), kleptoparasitism (Wittenberger and Hunt 1985), entombment (Brown and Brown 1996)).

3.1.3 Benefits of coloniality

The potential benefits of coloniality are less clear. If there is an ideal free distribution of individuals with respect to a clumped, limited resource, for example nesting-sites which provide protection from predators (they may be difficult to access (Robinson 1985) or used by another species which provides defense (Post 1994)), the consequence may be coloniality (Robinson 1985; Post 1994; Richardson 1997). Colonial living also increases the potential for the evolution of beneficial social behaviours (Crook 1964; Alexander 1974). Interest has focused on the sharing of information and cooperative defence in colonies. When food sources are patchy and ephemeral, colonies may act as information centres (Ward and Zahavi 1973) where individuals gain information concerning the location of the food patches from successful foragers (Brown 1988a). If colonies aid foraging group formation then an additional benefit may be passive (Brown 1988b) or active information transfer within foraging groups (Brown et al. 1991). Although some research has supported the information centre hypothesis (Emlen and Demong 1975; Brown 1986; Brown 1988a; Wilkinson 1992; Brown and Brown 1996), the issue remains a controversial one (Mock et al. 1988; Hagan and Walters 1990; Richner and Heeb 1995). Colonies may also provide protection from predation either as a result of enhanced communal vigilance (Hoogland and Sherman 1976) or predator mobbing (Wiklund and Andersson 1994; Tyler 1995) or as a result of the swamping of predators reducing per capita risk (Foster and Treherne 1981). However, these benefits must be viewed in the light of the potential attractiveness of colonies to predators.

3.1.4 Reproduction in colonies: costs and benefits?

The greater density and number of individuals in colonies may increase the potential for alternative reproductive strategies particularly intra-specific brood parasitism (Yom-Tov 1980; Møller 1987; Emlen et al. 1995; Brown and Brown 1996) and

extra-pair copulations (EPCs) (Møller 1987; Birkhead and Møller 1992) which may lead to high extra-pair paternity (EPP) (Westneat et al. 1990; Birkhead and Møller 1992; Richardson 1997). Extra-pair copulations offer some benefits to both males and females. While males may increase the number of offspring they father (Gibbs et al. 1990; Birkhead and Møller 1992), females may gain direct (e.g. paternal care: Davies 1992 or fertility assurance: Gray 1997) or indirect (Andersson 1994; Sheldon et al. 1997) benefits. However there may also be costs when extra-pair copulations are frequent. Males may have reduced assurance of paternity while females risk injury and harassment during forced EPCs (Birkhead and Møller 1992) and possibly reduced levels of paternal care (Dixon et al. 1994; Wright 1998). These costs and benefits are likely to vary between individuals, for example for males with age (Møller 1987; Morton et al. 1990; Richardson 1997), so high rates of EPP in colonies will neither be a universal cost nor benefit.

While some studies have reported an increase in the frequency of EPP with breeding density (Gowaty and Bridges 1991; Hoi and Hoi-Leitner 1997; Richardson 1997) the relationship is far from clear (Dunn et al. 1994; Birkhead 1998). Furthermore, a high frequency of EPP in colonies need not be a direct consequence of coloniality; increased opportunities for alternative reproductive strategies have been suggested to select for both male (Morton et al. 1990) and female driven (Wagner 1993; Wagner et al. 1996; Hoi and Hoi-Leitner 1997) colony formation.

3.2 AIMS

The central aim of this chapter is to investigate the maintenance of coloniality in the sociable weaver by testing how hypothetical costs and benefits of coloniality vary with colony size. When possible, direct measures of costs or benefits were used. When this was not possible indirect measures, expected to correspond to the cost or benefit, were used. The hypotheses for which predictions were tested were:

(1) Inefficient colonial foraging is a potential cost of coloniality (Hoogland and Sherman 1976; Hunt et al. 1986). Direct measurement of foraging efficiency was not possible so two indirect measures were used: (i) adult mass and size and (ii) relative chick mass (mass/tarsus). If foraging efficiency decreases with colony size then adult and/or chick masses are predicted to decrease with colony size.

(2) Colonial foraging is also a potential benefit of coloniality (Ward and Zahavi 1973). If foraging efficiency increases with colony size then adult and/or chick masses are predicted to increase with colony size.

(3) Colonies may attract nest predators (Wittenberger and Hunt 1985). If colonies do attract predators then the frequency of predator presence is predicted to increase with colony size.

(4) Colonies may provide defence against predators through communal vigilance and defence (Hoogland and Sherman 1976; Wiklund and Andersson 1994). The prediction that group mobbing must occur, for coloniality to provide protection against predators, was tested.

(5) Increased rates of parasite transmission are a potential cost of coloniality (Alexander 1974). If parasite transmission is a cost of coloniality then adult parasite load and/or chick parasite loads are predicted to increase with colony size.

(6) Coloniality may offer females more opportunities to dump eggs in the nests of conspecifics. If opportunities for intra-specific brood parasitism occur more frequently in colonies then the proportion of broods containing brood parasite chicks is predicted to increase with colony size.

(7) Colonies may offer birds more opportunities for extra-pair copulations (Morton et al. 1990). If the frequency of extra-pair copulations is greater in colonies then the proportion of broods containing extra-pair offspring is predicted to increase with colony size.

(8) Finally, to investigate the general implications of colony size for breeding success three measures of reproductive effort and three measures of reproductive output were used. The relationships between colony size and (i) clutch initiation date (first clutch), (ii) clutch size (first clutch) and (iii) egg volume (first clutch), (iv) brood size (first clutch), (v) fledging success (first clutch) and (vi) fledging success (annual) were investigated.

3.3 METHODS

The methods used for the collection of ringing and nest content data are given in chapter 1 while the methods used for the processing of genetic data are given in chapter 2.

Colony size was defined as the adult population size. To avoid pseudo-replication colony means were calculated. If data from different clutches were combined then group means were calculated from clutch means and these were used to calculate colony means. Correlations were calculated between dependent and independent

(colony size) variables using Spearman's rank correlation coefficient. One potential source of pseudo-replication is the repeated use of colonies in different years (colony 2 in all field seasons and colonies 10 and 11 in two years) however as colony size varied between years this may not be a serious problem. Table 3.1 details the numbers of adults, broods and clutches used in the calculation of colony means.

Where possible all correlations are reported separately for the three years of the study and then for the three years combined. If there was no significant effect of year on the dependent variable then means were pooled. If there was a significant effect of year then residuals were used to standardise the data before it was pooled.

3.3.1 Condition

Two sets of indirect measures were used to access foraging efficiency in the present study. They were adult morphometrics (Brown and Brown 1996) and chick mass (Hoogland and Sherman 1976; Møller 1987; Shields and Crook 1987; Brown and Brown 1996)

(a) Adult morphomterics

Three measures of adult morphology were used: (i) Mean adult mass at a colony (chapter 1). However, as adult mass (g) varied significantly with time elapsed between capture and ringing (mass = 27.2 - 0.005*(time in bag); $t = -7.23$, $n = 235$, $p < 0.001$) it was necessary to correct for time in the bag by taking residuals from this regression. The observed correlation between mass and time in the bag was not due to lighter birds living in larger colonies as the relationship was also significant within two out of four large (population > 20) colonies. Time spent in the bag was only recorded for birds ringed in 1998 and therefore only these measurements were used. (ii) Mean adult wing length (mm) at a colony (chapter 1). (iii) Mean adult tarsus length (mm) at a colony (chapter 1).

(b) chick mass

Mean chick mass was calculated for each brood of chicks weighed and measured at age 9 - 15 days. In order to control for age each chick's mass was expressed as a residual from a regression of mass against tarsus length ($df = 178$, $p < 0.001$, $r^2 = 0.551$). Mean chick mass in a brood did not vary significantly with brood size (ANOVA: $F_{4,78} = 0.52$, $p = 0.72$) or brood order (ANOVA: $F_{2,80} = 2.88$, $p = 0.062$) so data from clutches of all sizes were pooled but as the effect of brood order approached significance, data were analysed for first broods alone and for all broods combined. Mean chick mass in a clutch varied significantly between years

Table 3.1 (a). Summary of data collection (estimated colony size (number of adults) and numbers of: incubated clutches; breeding groups; broods used for DNA analysis; broods with known social parents) during the first field season (October 1995-April 1996). In the totals column, values with subscript a refer to additional clutches collected at other colonies. In the row reporting the number of broods with identified parents, values without a subscript refer to the number of broods with parents confirmed by capture and provisioning records while values with subsript c record the number of cases in which the identity of adults was determined by capture alone. (s.p. = social parents)

Colony :	1	2	3	4	5	6	7	8	9	total
Estimated size	2	29	3	3	1	3	7	3	9	-
incub. clutches	2	29	3	3	1	3	7	3	9	60
breeding groups	2	22	3	2	1	3	5	3	7	48
DNA analysis	0	0	0	0	1	1	3	0	0	5, 1a
broods with known s. p.	_	_	_	_	1c	1c	3c	_	_	5c, 1a

Table 3.1 (b) Summary of data collection (estimated colony size (number of adults) and numbers of: incubated clutches; breeding groups; broods used for DNA analysis; broods with known social parents) during the second field season (January 1997 - June 1997). In the row reporting the number of broods with identified parents, values without a subscript refer to the number of broods with parents confirmed by capture and provisioning records while values with subsript c record the number of cases in which the identity of adults was determined by capture alone. (s.p. = social parents)

Colony :	2	10	11	15	17	20	21	22	total
Estimated size	30	14	13	16	4	22	4	2	-
incub. clutches	21	14	8	16	5	8	2	1	75
breeding groups	10	6	4	6	3	6	2	1	38
DNA analysis	19	10	5	5	-	3	1	0	43
broods with known s.p.	8,2c	_	1c	1	_	2	_	_	11,3c

Table 3.1 (c) Summary of data collection (estimated colony size (number of adults) and numbers of: adults ringed; incubated clutches; breeding groups; broods used for DNA analysis; broods with known social parents) during the third field season (November 1997 - May 1998). In the row reporting the number of clutches with identified parents, the top value is the total number, the lower number (subsript c) is the number of cases in which the identity of those adults was determined by capture. (s.p. = social parents)

Colony :	2	10	11	12	23	24	25	27	28	29	30	31	32	33	34	35	total
Estimated size	26	16	15	7	5	34	15	27	40	4	2	26	14	6	10	4	-
adults ringed (mass/parasites)	23	13	12	7	5	27	8	24	40	2	1	25	14	5	6	4	216
incub. clutches	7	4	2	3	3	1	4	9	5	4	1	8	5	2	3	4	65
breeding groups	7	3	2	2	3	1	4	8	4	2	1	8	5	3	3	3	59
DNA analysis	5	3	2	2	2	-	2	-	-	2	-	8	2	1	-	1	30
broods with known s.p.	4	2	1,1c	_	2	_	2	_	_	1	_	_	_	_	_	_	13,1c

(ANOVA: $F_{2,80} = 13.4$, $p < 0.001$) so the residuals from this ANOVA were used to standardise for the effect of year.

3.3.2 Predation

(a) Predator encounter rate

Predation rate is difficult to measure because of uncertainty over the fate of lost clutches. Snakes are probably the most important predator on chicks and eggs in the sociable weaver (Maclean 1973). So, in the present study the probability of encountering a large snake (length > 1 metre; boomslangs *Dispholidus typus* and black mambas *Dendroaspis polylepis)* at a colony was used to estimate the attractiveness of colonies to snakes. As encounter rate is determined by the arrival rate of snakes at a colony and the length of time they spend there (likely to be proportional to colony size) a correction for colony structure size (number of chambers) was included in the calculation of estimated arrival rate:

$$\text{arrival rate for colony} = \frac{\text{visits to colony when snake present}}{(\text{total visits to colony}) \times (\text{colony structure size})}$$

I visited each colony 14, 15 and 11 times during the first, second and third field seasons respectively.

(b) Response to predators

Qualitative observations of the responses of sociable weavers to natural predators were collected during behavioural watches (Chapter 2 for details). No data were collected on the magnitude of mobbing in relation to colony size.

3.3.3. Ecto-parasite load

Three direct measures of ecto-parasite load were calculated: (i) The mean adult parasite load per colony was calculated as the mean number of feather lice (family Pthiraptera) recovered from each adult at a colony during ringing in 1998. (ii) Mean chick parasite load was calculated as the mean number of dermestid larvae per chick in each clutch checked between age 9 and 15 days. Transformed ($\sin^{-1}(\sqrt{x})$) mean chick parasite load did not vary significantly between years (ANOVA: $F_{2,68} = 1.29$, $p = 0.282$), with clutch order (ANOVA: $F_{2,67} = 0.18$, $p = 0.839$) or with brood size (ANOVA: $F_{4,65} = 0.45$, $p = 0.773$) so all years and clutches were pooled for the analysis of colony size effects. (iii) The proportion of parasitised broods at a colony was defined as the proportion of all broods at a colony in which at least one chick was parasitised by dermestid larvae.

3.3.4 Alternative reproductive strategies

(a) Intra-specific brood parasitism

Using molecular data from chapter 2, the mean proportion of sampled broods including at least one case of intra-specific brood parasitism (IBP) was calculated for each colony. Additionally, the total proportion of IBP chicks was calculated for each colony.

(b) Extra-group paternity

Following chapter 2, extra-group paternity is used in place of extra-pair paternity. Using molecular data from chapter 2, the mean proportion of sampled broods including at least one case of extra-group paternity was calculated for each colony. Additionally the proportion of chicks with an extra-group father was calculated for each colony.

3.3.5 Reproductive effort and success

Three measures of reproductive effort and success were used. Data were pooled across years. When there was a significant effect of year, residuals from an ANOVA with year as factor were used to standardise the data before they were pooled.

(a) Reproductive behaviour

The three measures of reproductive effort were: (i) Median first incubated clutch lay date at a colony. Median first clutch initiation date varied significantly between years (Kruskal Wallis: $H = 28.1$, $df = 2$, $p < 0.001$). (ii) Mean first incubated clutch size at a colony. Mean first clutch size varied significantly between years (ANOVA factor year: $F_{2,137} = 9.06$, $p < 0.001$). (iii) Mean egg volume for first incubated clutches at a colony. An egg volume index was calculated by multiplying the breadth squared by the length (Chapter 1). Mean first clutch egg volume did not vary significantly between years (ANOVA factor year: $F_{2,136} = 1.00$, $p = 0.37$).

(b) Reproductive success

The three measures of reproductive success were : (i) Mean first incubated clutch brood size at a colony. Mean first clutch brood size varied significantly between years (ANOVA factor year: $F_{2,142} = 3.37$, $p = 0.037$). (ii) Mean number of chicks fledged from first incubated clutches at a colony. Mean fledging success per first clutch did not vary significantly between years (ANOVA factor year: $F_{2,142} = 0.05$, $p = 0.95$). (iii) Mean total number of chicks fledged per group over the breeding

season at a colony. The total number of chicks fledged per group over each breeding season varied significantly between years (ANOVA factor year: $F_{2,142}$ = 9.11, $p < 0.001$).

3.4 RESULTS

3.4.1 Condition

(a) Adult morphometrics

Neither mean adult mass nor dimensions (tarsus and wing length) were significantly correlated with colony size (Figure 3.1.a,b,c; Table 3.2). In addition, the mean of adult mass controlling for body size was not significantly correlated with colony size (r_s = 0.019, n = 23, NS).

(b) Chick mass

Mean chick mass showed a negative trend with colony size. This correlation was not significant either in individual years or for all years combined when only first clutches were considered. However, when all clutches were included it was significant (Figure 3.2; Table 3.3).

Based on data from years two and three chick mass may have important implications for reproductive success. Chicks which eventually died (mean residual (controlling for age) = -0.110±0.312) weighed less than those which fledged (mean residual (controlling for age) = 0.962±0.284). The difference was significant (ANOVA: $F_{1,122}$ = 6.46, p = 0.012).

3.4.2 Predation

(a) Predator encounter rate

Most depredation of sociable weaver nests at the study site appeared to be by large snakes particularly the boomslang. During the study period 466 weekly visits were made to the colonies. On seven of these visits a snake was encountered at the colony (0.015 large snakes/colony visit). A similar frequency was recorded for encounters with large snakes during a more wide ranging colony survey (Chapter 5; 4 snakes recorded at 272 active colonies; 0.015 snakes/colony visit). In every case that a large snake was observed at a colony when the colony was re-checked all formerly active nests (containing eggs or chicks) were found to have been depredated.

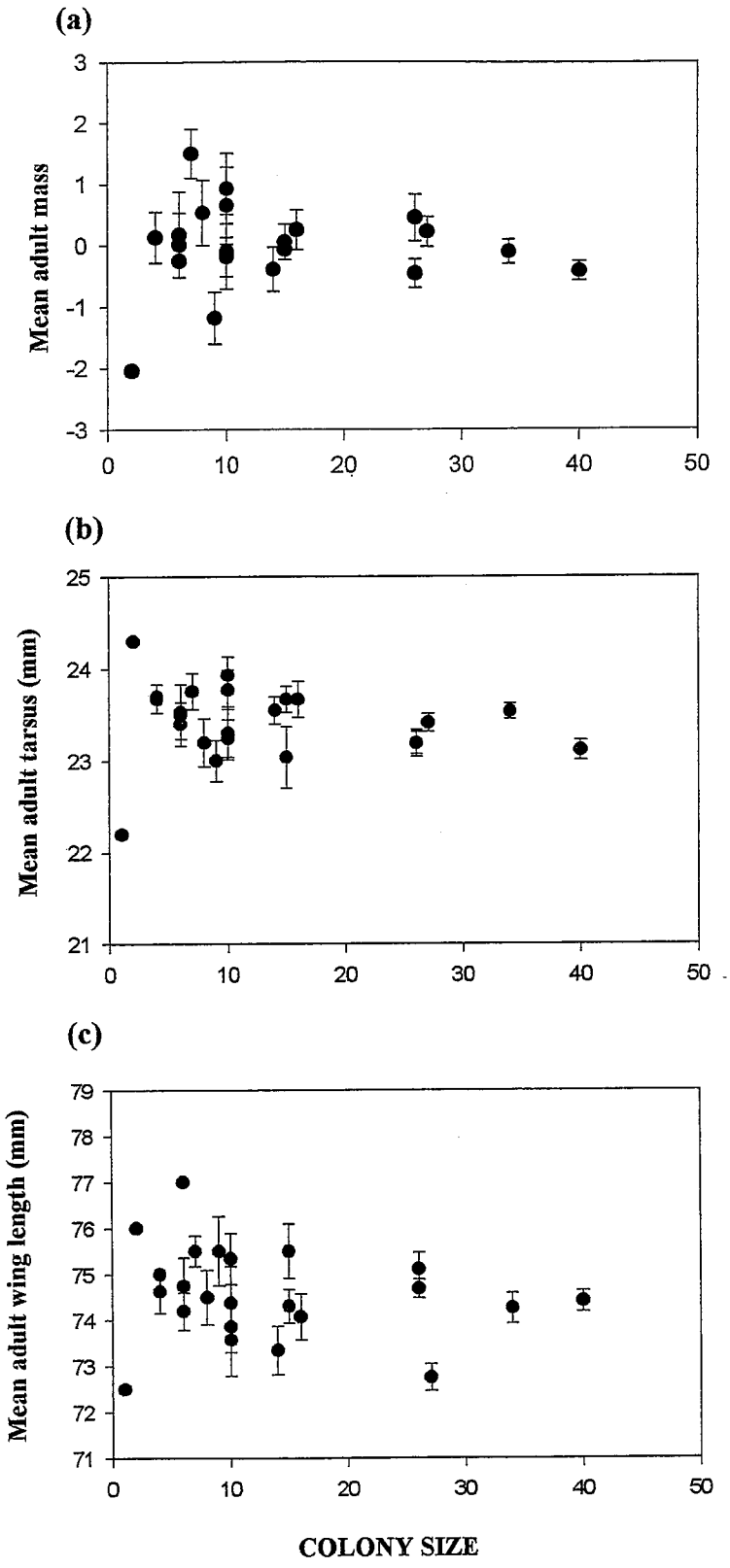


Figure 3.1. Effect of colony size on: (a) mean adult mass (r_s= -0.021, n = 21, Ns); (b) mean adult tarsus length (r_s= -0.241, n = 23, NS); (c) mean adult wing length (r_s= -0.256, n = 23, NS).

Table 3.2 Correlations between colony size and adult morphometrics. All values are Spearman's rank correlation coefficients, the number of colonies used is given in brackets.

Variable	Spearman's rank correlation coefficient between variable and colony size			
	Year 1	Year 2	Year 3	Combined
mean wing length	-0.28, (7), NS	-0.21, (7), NS	-0.26, (23), NS	-0.26, (37), NS
mean tarsus length	0.27, (7), NS	0.23, (7), NS	-0.24, (23), NS	-0.12, (37), NS
mean adult mass	-	-	-0.02, (21), NS	-

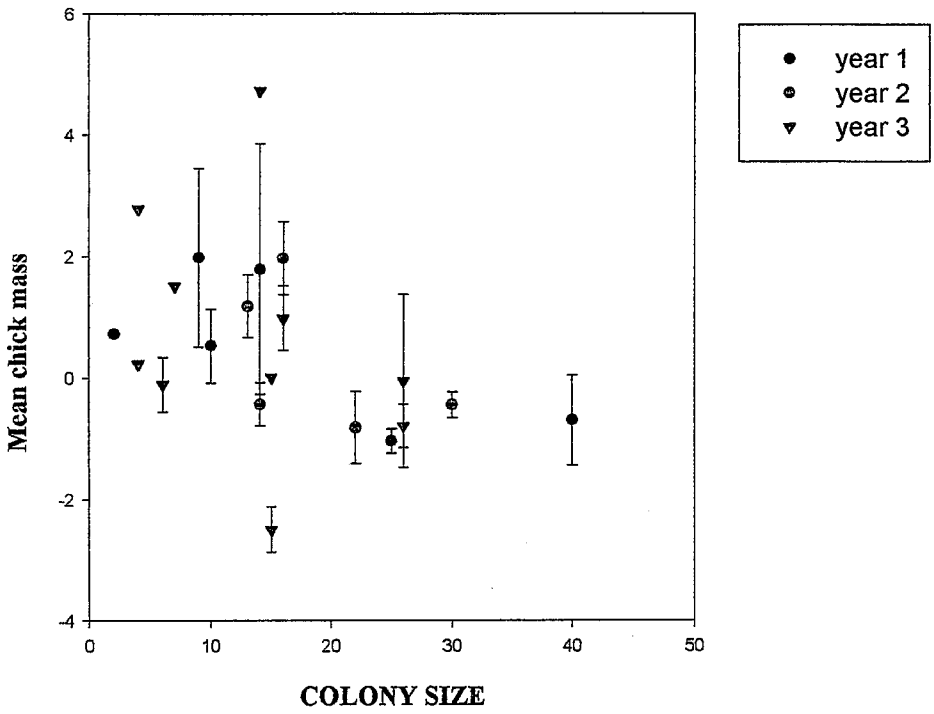


Figure 3.2 Effect of colony size on mean chick mass (r_s = -0.549, n = 20, $p < 0.02$). Values for mean chick mass were standardised for age for the effect of year.

Table 3.3 Correlations between colony size and chick mass. Chick mass was corrected for age by taking residuals from a regression of mass against tarsus. All values are Spearman's rank correlation coefficients, the number of colonies used is given in brackets.

Variable	Spearman's rank correlation coefficient between variable and colony size			
	Year 1	Year 2	Year 3	Combined
mean chick mass (first clutches only)	-0.49, (6), NS	0.20, (4), NS	-0.47, (9), NS	-0.35, (19), NS
mean chick mass (all incubated clutches)	-0.66, (6), NS	-0.60, (5), NS	-0.45, (10), NS	-0.55, (21), **$p < 0.02$**

Large colonies seemed to attract more snakes as the frequency of encounter (snakes/chamber/visit) was significantly positively correlated with colony size (r_s = 0.539, n = 31, $p < 0.005$; Figure 3.3).

Other potential predators of sociable weaver chicks and eggs included an unidentified nocturnal snake species and the gymnogene *Polyboroides typus* which on one occasion was observed attempting to plunder a sociable weaver nest (pers. obs.).

(b) Response to predators

Sociable weavers mob rosy faced lovebirds *Agapornis roseicollis* (Chapter 2), pygmy falcons *Polihierax semitoquartus* (pers. obs.; M. Trewby, pers. comm.), suricats *Suricata suricatta* (M. Trewby, pers. comm.) and model snakes (pers. obs.; M. Trewby, pers. comm.). However they were observed to ignore a large boomslang plundering nest chambers.

3.4.3 Ecto-parasite load

There was a significant positive correlation between mean adult ecto-parasite load (number of feathermites per adult) and colony size (Figure 3.4.a; Table 3.4). However, there was no relationship between number of feathermites and adult mass (controlling for time in bag) using linear regression (t-test: t = -0.33, df = 231, p = 0.744).

There was no significant correlation between mean chick parasite load (number of dermestid larvae per chick) and colony size (Figure 3.4.b, Table 3.4). Nor was the proportion of parasitised clutches in a colony significantly correlated with colony size (Table 3.3). Parasite load did not have a significant effect on chick mass (controlling for age) using linear regression (t-test: t = -1.43, df = 83, p = 0.157).

3.4.4 Alternative reproductive strategies

(a) Intra-specific brood parasitism

Neither the proportion of clutches containing IBP chicks (Figure 3.5.a; r_s = 0.289, n = 13, NS) nor the total proportion of IBP chicks (r_s = 0.343, n = 13, NS) were significantly correlated with colony size.

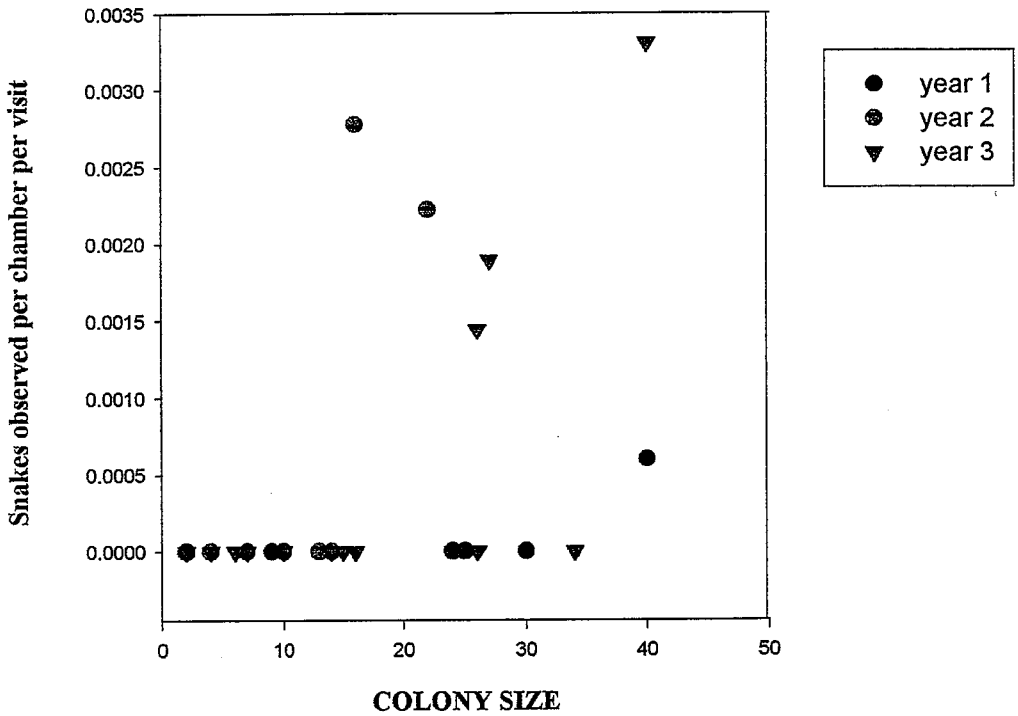


Figure 3.3 Effect of colony size on probability (measured as snakes/ chamber/visit) of observing a large snake at the colony ($r_s = 0.54$, $n = 32$, $p < 0.002$).

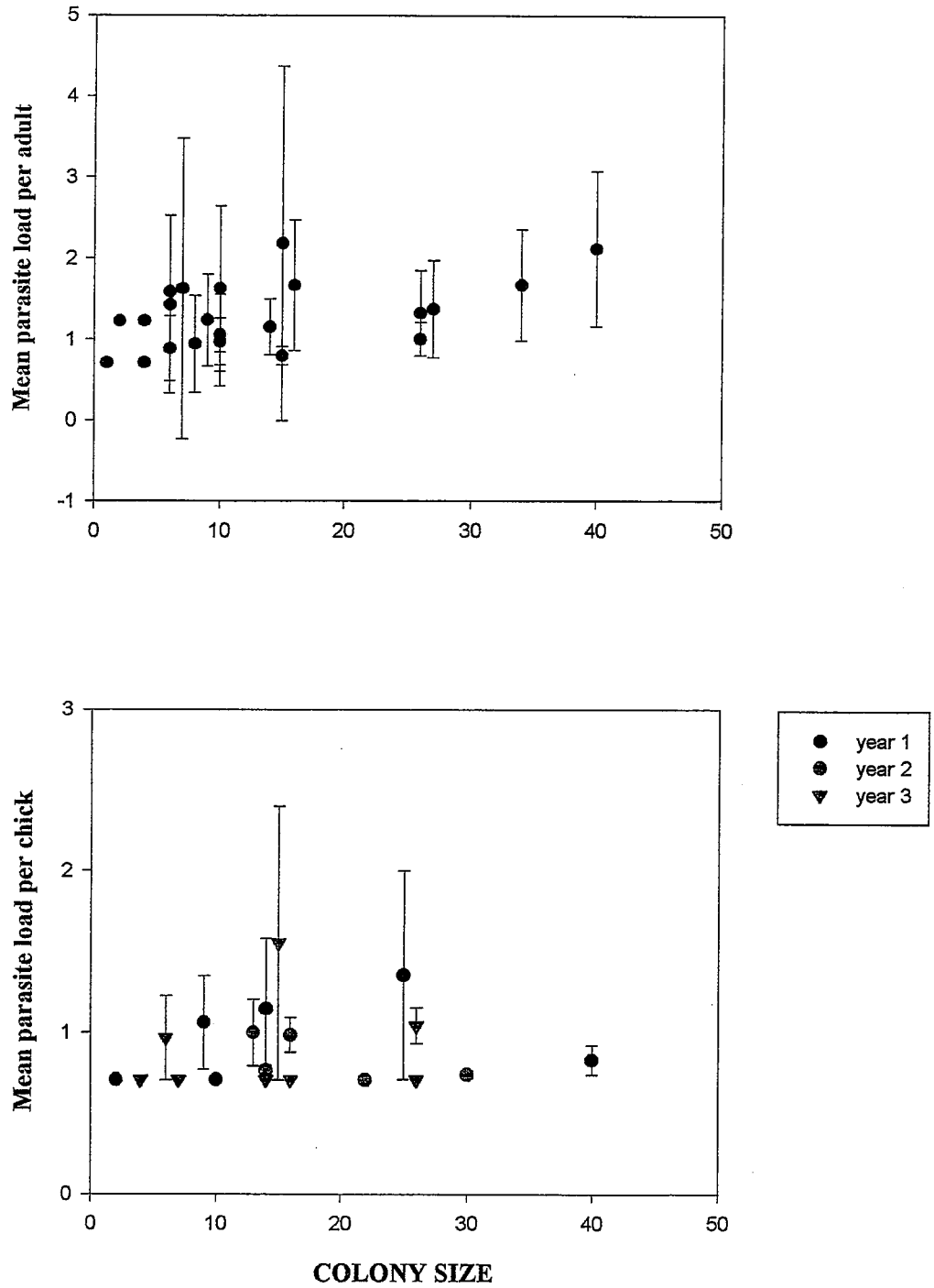


Figure 3.4 Effect of colony size on: (a) mean parasite load per adult (r_s= 0.457, n = 23, $p < 0.05$); (b) mean parasite load per chick (r_s= 0.263, n = 21, NS).

Table 3.4. Correlations between colony size and adult and chick parasite loads. Adult parasite load is the mean number of feather lice recorded per adult. Chick parasite load is the mean number of specimens of *Dermestes* larvae recorded per chick (chick age: 9-15 days). All values are Spearman's rank correlation coefficients, the number of colonies used is given in brackets.

Variable	Spearman's rank correlation coeffient between variable and colony size (n = number of colonies).			
	Year 1	Year 2	Year 3	Combined
mean adult parasite load	-	-	0.46, (23), **$p < 0.05$**	-
mean chick parasite load (all clutches combined)	0.49, (6), NS	-0.80, (5), NS	0.28, (9), NS	0.26, (20), NS
proportion of clutches parasitised	0.20, (6), NS	-0.60, (5), NS	0.31, (9), NS	0.24, (20), NS

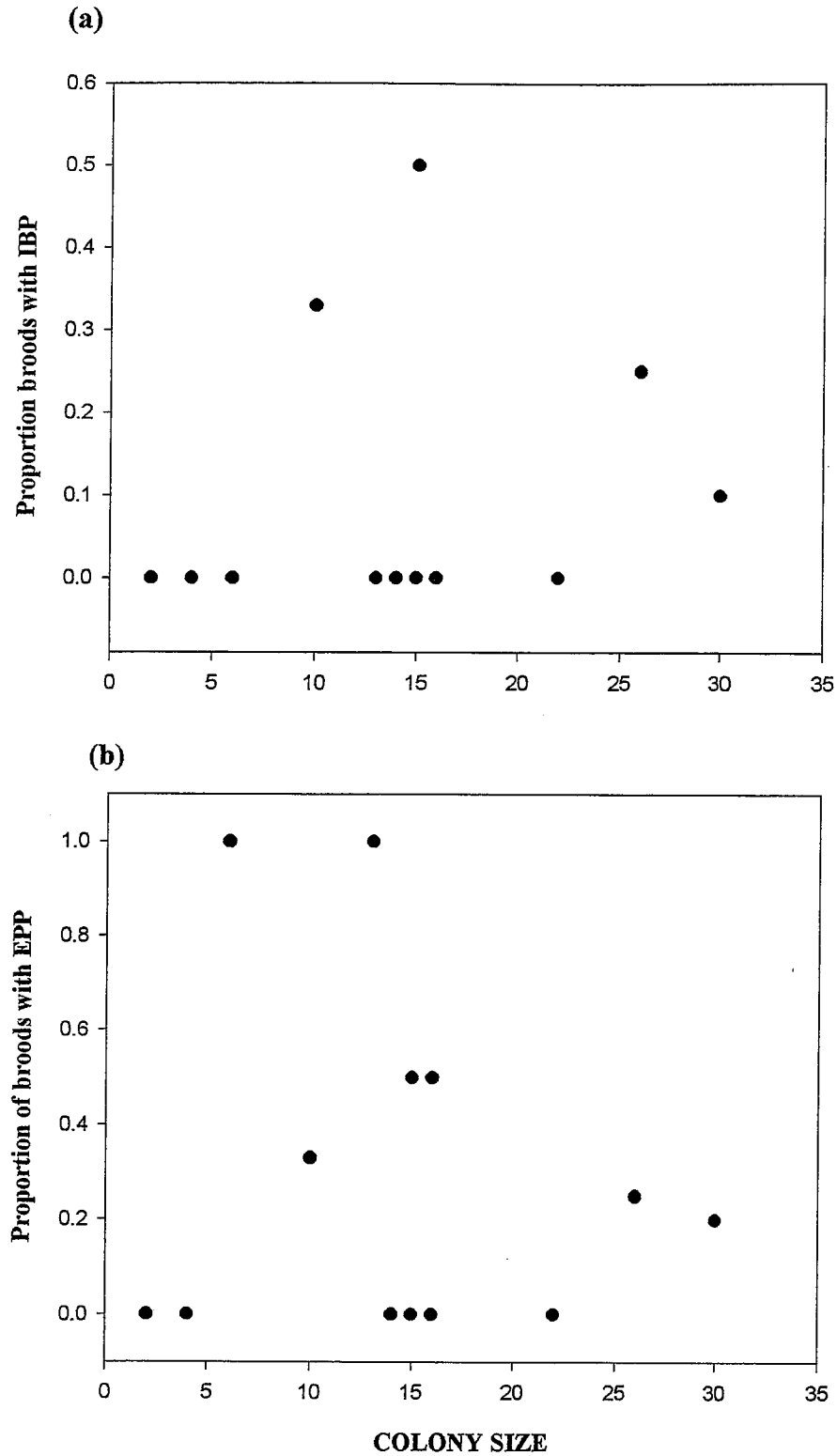


Figure 3.5 Effect of colony size on: (a) the proportion of broods containing IBP offspring ($r_s = 0.289$, n = 13, NS); (b) the proportion of broods containing EPP offspring ($r_s = 0.035$, n = 13, NS).

(b) Extra-group paternity

Neither the proportion of clutches containing extra-group paternity (Figure 3.5.b; r_s = -0.035, n = 13, NS) nor the total proportion of extra-group chicks (r_s = 0.141, n = 13, NS) were significantly correlated with colony size.

3.4.5 Reproductive effort and success

The three measures of reproductive behaviour (Figure 3.6, Table 3.5) did not show clear correlations with colony size. Synchrony is not a confounding factor in these analyses as it did not correlate with colony size (r_s = 0.232, n = 29, NS). Additionally, the three measures of reproductive success did not show clear correlations with colony size (Figure 3.7, Table 3.6). Nor did the coefficient of variation of the total number of chicks fledged per group correlate significantly with colony size (r_s = 0.246, n = 33, NS).

3.5 DISCUSSION

Six main results are presented in this chapter (1) Adult mass did not vary with colony size. However, chicks were significantly lighter in larger colonies. (2) Larger colonies were significantly more attractive to snakes. (3) Adults but not chicks had a significantly greater ecto-parasite load at larger colonies. (4) The frequency of clutches containing IBP offspring did not vary with colony size. (5) The frequency of clutches containing extra-pair paternity did not vary with colony size. (6) Three measures of reproductive behaviour and three measures of reproductive success did not show a consistent pattern with colony size.

3.5.1 Costs and benefits of coloniality in the sociable weaver

(a) Foraging and colony size

Mean chick mass was lower in large colonies. This suggests, but does not prove, that foraging efficiency decreases with colony size. The reduction in mean chick mass with colony size may have been the result of reduced foraging success due to resource depletion (as is suggested by the increase in travel distance with colony size in the cliff swallow (Brown and Brown 1996)) or reduced foraging efficiency (Milinski and Parker 1991). However, variation in chick mass may also result from: variation in provisioning rate independent of food availability (for example as a response to paternity (Burke et al. 1989) - although the proportion of EPP chicks did not increase with colony size in the present study; genetic differences between chicks (Coulson et al. 1998; Coltman et al. 1998); or variation in a second factor

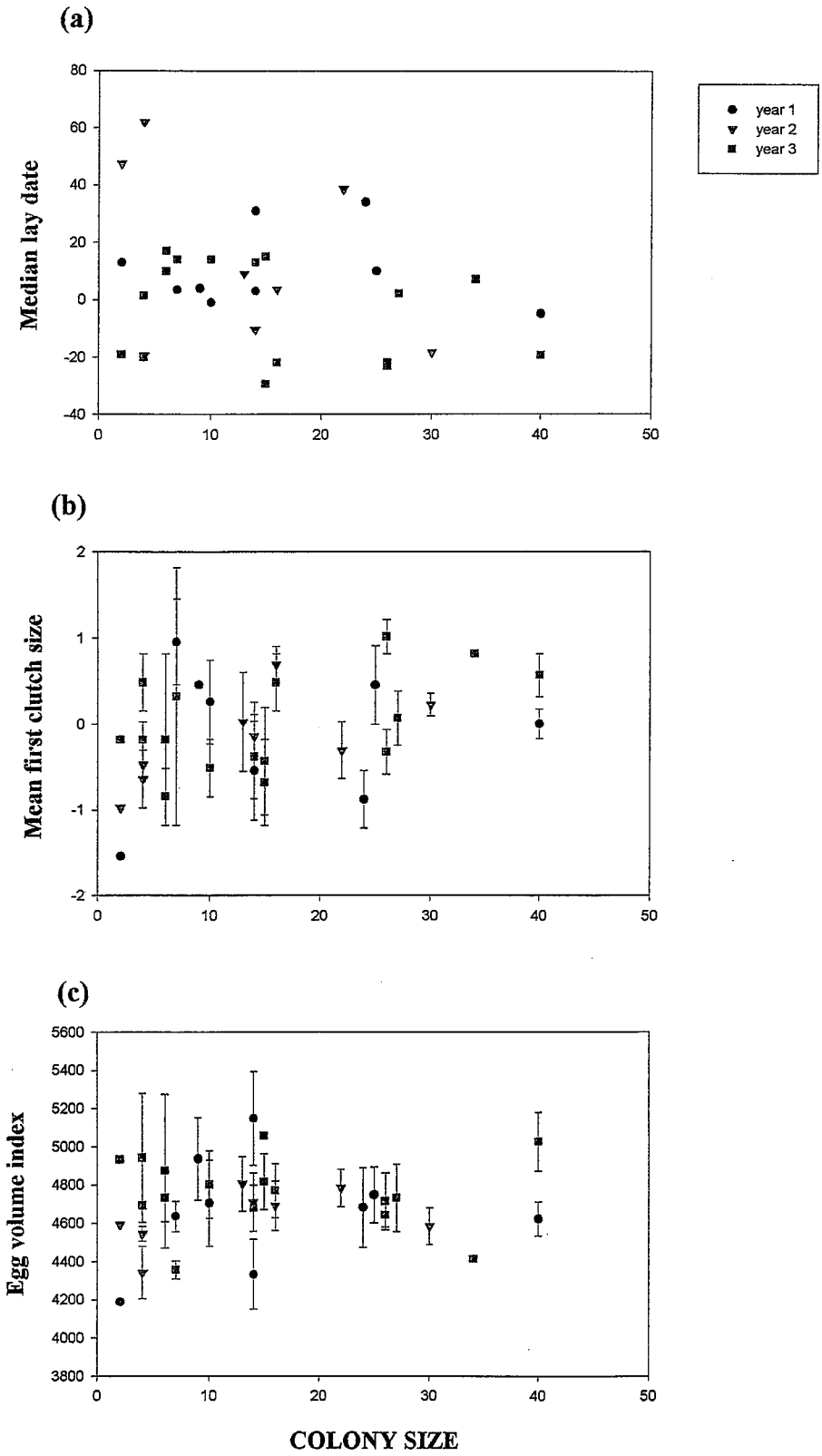


Figure 3.6. Effect of colony size on three measures of reproductive effort: (a) date of median first clutch initiation standardised for year (r_s= -0.256, n = 33, NS); (b) mean first clutch size standardised for year (r_s= 0.390, n = 33, $p < 0.05$.); (c) mean egg volume (r_s= 0.082, n = 33, NS).

Table 3.5 Correlations between colony size (adult population) and three measures of reproductive effort. All values are Spearman's rank correlation coefficients, the number of colonies used is given in brackets.

Variable	Spearman's rank correlation coefficient between variable and colony size (n = number of colonies)			
	1996	1997	1998	Combined
median lay date of first clutch	-0.11, (9), NS	-0.53, (9), NS	-0.21, (15), NS	-0.27, (33), NS
mean size of first clutch	-0.03, (9), NS	0.36, (9), NS	0.44, (15), NS	0.39, (33), **$p < 0.05$**
mean egg volume (first clutch)	0.18, (9), NS	0.36, (9), NS	-0.14, (15), NS	0.08, (33), NS

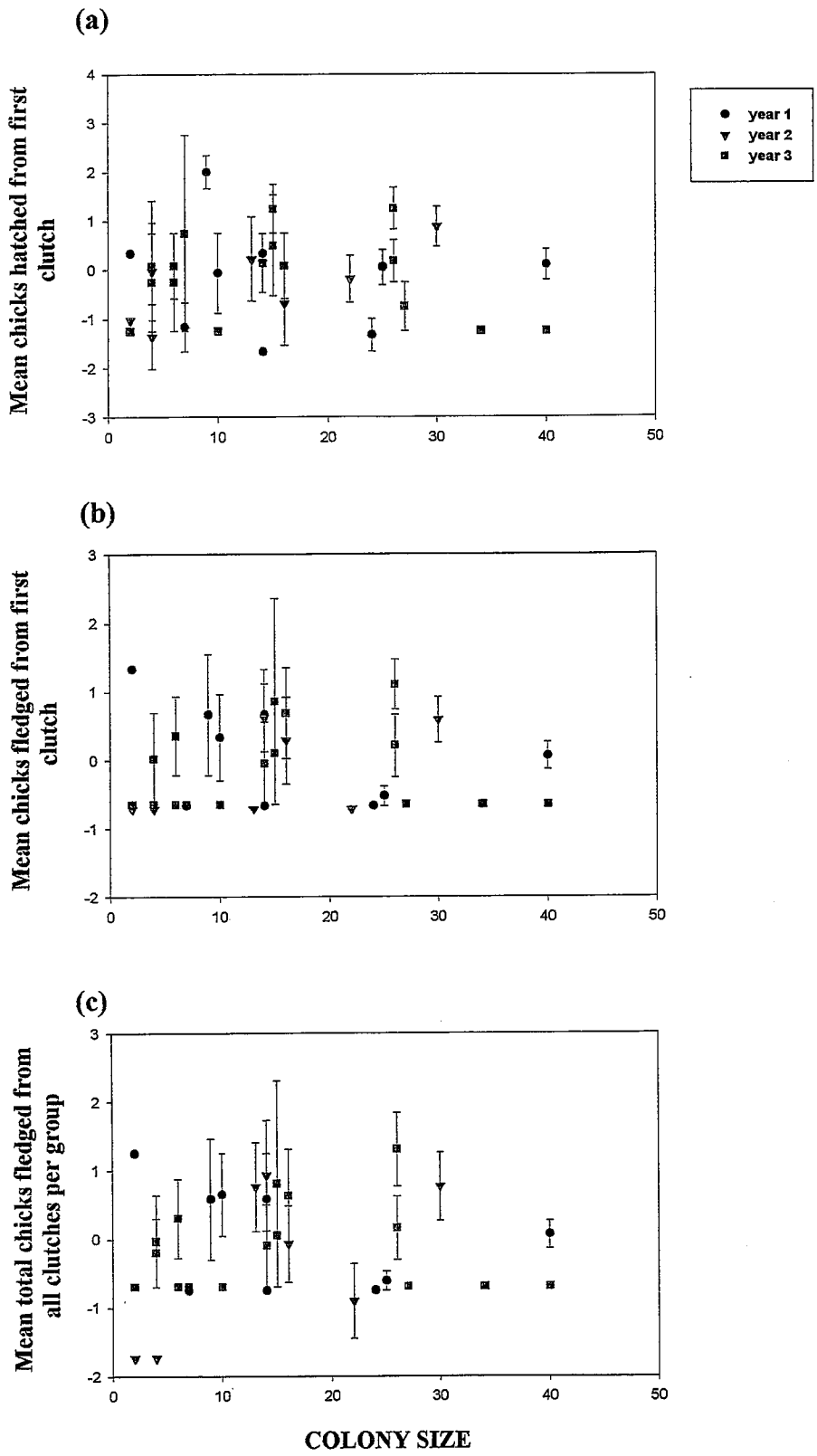


Figure 3.7 Effect of colony size on three measures of reproductive success: (a) mean chicks hatched from first clutch standardised for year (r_s= 0.093, n = 33, NS); (b) mean chicks fledged from first clutch (r_s= 0.202, n = 33, NS); (c) mean chicks fledged per 'pair' from all clutches combined (r_s= 0.198, n = 33, NS).

Table 3.6 Correlations between colony size (adult population) and three measures of reproductive success. All values are Spearman's rank correlation coefficients, the number of colonies used is given in brackets.

Variable	Spearman's rank correlation coefficient between variable and colony size (n = number of colonies)			
	1996	1997	1998	Combined
mean chicks hatched/ clutch (first clutches)	-0.23, (9), NS	0.46, (9), NS	0.01, (15), NS	0.09, (33), NS
mean chicks fledged / clutch (first clutches)	-0.38, (9), NS	0.61, (9), NS	0.14, (15), NS	0.20, (33), NS
mean chicks fledged/group (all clutches)	-0.39, (9), NS	0.57, (9), NS	0.05, (15), NS	0.20, (33), NS

(for example age at which brood reduction occurs or parasite load - although chick parasite load did not increase with colony size in the present study).

Mean adult mass did not show the same pattern of decrease with colony size. However adult and chick mass may indirectly measure differ aspects of foraging success because there are differences between adult and juvenile diets (Maclean 1973; Ferguson 1988) or because adult mass does not reliably describe condition if birds trade-off energy storage and predation risk (Cuthill and Houston 1997).

(b) Predation and colony size

Large snakes, known to be nest predators, were encountered more often at large than small colonies. In the present study, all the active chambers in colonies visited by snakes were depredated. Maclean (1973) also found that snakes frequently rob an entire nest mass; on one occasion a cape cobra *Naja nivea* removed 36 chicks and 17 eggs from a colony at his study site in the Kalahari. Therefore, the cost of attracting snakes may be very high in the sociable weaver. Indeed, over all colonies a 1.5% probability of encountering a snake on a random colony visit translates to approximately a 40% chance a snake will visit a colony during a breeding attempt (based on the assumption of 35 independent days the rough probability that a nest is depredated is $(1 - (0.985)^{35} = 0.411)$). The assumption of independence is not strictly valid because all 35 days are consecutive and at the same colony. In the present study the cost of predation appeared to be disproportionately paid by large colonies.

The correlation between antipredator behaviour and colony size was not investigated but it is unlikely that colonial breeding provides protection against large snakes. Although some colony members did mob or alarm call at intruders (Chapter 2) they do not deter snakes (Maclean 1973; M. Trewby pers. comm.; pers. obs.). Predator swamping is also unlikely to be a benefit of coloniality as all nests were depredated.

(c) Ecto-parasite load and colony size

Adults living in larger colonies carried significantly more feather lice than adults living in smaller colonies in the present study. But chicks in larger colonies were not parasitised by more dermestid larvae than those in small colonies. Nor was the proportion of broods with parasites greater in large colonies.

The magnitude of the cost of parasitism for sociable weavers is uncertain (Maclean 1973). In the present study, no decrease in either chick or adult mass was found with increasing parasite load. However, some studies in other species report clear

costs of parasitism (e.g. Brown and Brown 1996). An additional concern regarding the data is that the counts of at least two other species of ectoparasites found on adults (one a hippoboscid fly, the other a haematophagus mite; chapter 1) could not be assessed in the field and were not included in the analyses.

(d) Alternative reproductive strategies

The frequency of intraspecific brood parasitism was not greater in large sociable weaver colonies. As there are many active nests and hence presumably many opportunities for brood parasitism in large colonies this suggests that either female sociable weavers rarely attempt brood parasitism or that there are effective defences against it. It is possible that the continuous incubation described by Maclean (1973) is one of these defences.

The frequency of extra-group paternity was not greater in large sociable weaver colonies. This fits the general pattern emerging from avian studies (Birkhead 1998); although high breeding densities may facilitate high rates of extra-pair paternity (Gowaty and Bridges 1991; Hoi and Hoi-Leitner 1997; Richardson 1997), high breeding densities do not consistently lead to high frequencies of extra-pair paternity (Dunn et al. 1994). Indeed, the relationship between high breeding density and high frequency of extra-pair paternity often seems to be manifested through high local variance in 'quality' in areas of high local density (Morton et al. 1990; Wagner et al. 1996; Richardson 1997). Although the results presented in this study suggest that extra-group copulations are not more frequent in large sociable weaver colonies, it is important to note, the available sample sizes were small for both colonies (n = 13) and broods (n = 33).

(e) Reproductive effort, reproductive success and colony size

Of the three measures of reproductive behaviour used in this study median first clutch date and mean egg volume were not correlated with colony size. Mean first clutch size increased with colony size. If females optimise clutch size (Pettifor et al. 1988; Daan et al. 1990; Lessells 1991) then larger clutches may indicate a benefit of large colony size. The three measures of reproductive success did not vary significantly with colony size. There is no *a priori* reason to predict a monotonic relationship and when the costs and benefits of coloniality trade off against each other then reproductive success may be greatest at intermediate sized colonies (Brown and Brown 1996). However, this study provides no evidence of greater reproductive success at intermediate sized colonies.

3.5.2 The sociable weaver in context

The equilibrium approach to the maintenance of group living is open to several lines of criticism. Perhaps the most important of which being that it is correlative and hence liable to be confounded by variation in individual quality between colonies (unless experimental manipulation is attempted). Indeed some studies have shown that individuals vary in fundamental ways between colonies (e.g. age (Vessems and Draulans 1986; Shields and Crook 1987)). However in the sociable weaver most adults are colony faithful and the frequency of natal philopatry is high (Maclean 1973) so birds are unlikely to select colonies and the equilibrium approach is probably valid.

The results of the present study, and of six comparable studies on other species, support a general pattern of reduced chick mass and high ectoparasite loads at large colonies (Table 3.7). They also suggest that the consequences of coloniality for predation rate depend largely upon the ecology of predator and prey.

Brown (1986; 1988a,b) has provided evidence that group foraging is advantageous for cliff swallows *Hirundo pyrrhonata.* However there is little general evidence that foraging efficiency is greater at large colonies either in the cliff swallow (Brown and Brown (1996) found that adult cliff swallows living in large colonies are not in better condition than those living in small colonies); or over a range of species (in five out of seven studies in Table 3.7, chick mass was lower or chick starvation rates higher in larger colonies). Thus, foraging success may be lower at large colonies (e.g. as a result of reduced resource availability (Brown and Brown 1996) or increased interference (Wittenberger and Hunt 1985)) or increased foraging efficiency may fail to balance the cost of parasitism (Hoogland and Sherman 1976; Shields and Crook 1987; Brown and Brown 1996). Increased ecto-parasite loads are a consistent correlate of coloniality across the range of species studied (Table 3.7).

The consequences of colony size for predation rate depends upon both the attractiveness of colonies for predators and the effectiveness of group defences. For example, for nestling fieldfares *Turdus pilaris* predation rate decreased with colony size because defecation (soiling predator's feathers) makes mobbing by adult fieldfares an effective defence at large colonies (Wiklund and Anderson 1994). But when fiedfares nest in areas inhabited by tawny owls *Strix aluco,* adult fieldfare survival decreased with colony size. This was presumably because colonies attract owls which feed at night when mobbing is not possible (Wiklund

Table 3.7: Patterns of correlation between colony size and potential costs and benefits of coloniality (including indices measuring foraging success, predation, parasitism and reproductive success). All correlations show the effect of increasing colony size.

Study species and reference	Foraging success - adult mass	Foraging success - chick mass	Predator attraction	Group defence	Ecto-parasite load	Clutch size	Fledging success	Extra-pair paternity	Intra-specific brood parasitism
(i) Bank swallow Hoogland and Sherman (1976)	-	Decreased	-	Detection distance + mobbing effort increased	Increased	-	-	- (but no increase in attempts with dummy)	Never recorded
(ii) Grey heron Vessems and Draulans (1986)	-	- (but fewer large chicks)	Predation rate low	No mobbing observed	-	No correlation	Number large chicks decreased	-	-
(iii) Barn swallow Møller (1987)	-	No correlation (but feeding of chicks decreased)	-	Detection distance increased	Proportion nests infected increased	No correlation	-	- (but EPCs and chases increased	Increased
(iv) Barn swallow Shields and Crook (1987)	-	No correlation	-	-	increased for nestlings	decreased	decreased	-	-
(v) Fieldfare Wiklund and Andersson (1994)	-	- (but higher chick starvation)	Greater adult predation (by tawny owls)	increased mobbing + decreased chick predation	-	-	Increased with colony size in the absence of tawny owls	-	-
(vi) Cliff swallow Brown and Brown (1996)	Annual variation in correlation	No correlation (but higher chick starvation)	Increased	Detection distance increased	Increased for nests, nestlings	No correlation	Generally greatest at intermediate colonies	No data (but EPC attempts increased)	Increased
(vii) Sociable weaver This study (1998)	No correlation	Decreased	Increased (for nest predators)	- (but mobbing is observed)	increased for adults (not nestlings)	Increased	No correlation	No correlation	No correlation

and Andersson 1994). Thus, in some conditions increasing colony size may aid the deterrence (Hoogland and Sherman 1976) or swamping (Foster and Treherne 1981) of predators but if these benefits outweigh the cost of predator attraction (Brown and Brown 1996) depends upon the ecology of predators and prey.

No studies report increasing fledging success with colony size and only two studies provide evidence indicative of optimal intermediate colony sizes (Wiklund and Andersson 1994; Brown and Brown 1996). Thus only these two studies provide an explanation for the maintenance of coloniality. Two other studies report a reduction in fledging success with colony size (Vessems and Draulans 1986; Shields and Crook 1987). On the basis of their result Shields and Crook (1987) suggest that, despite a net cost of coloniality, barn swallows *Hirundo rustica* are forced into colonies as a result of nest site limitation.

The results of the present study do not provide a clear explanation of the maintenance of coloniality in the sociable weaver. Although considerable costs were described (lower chick mass, higher ectoparasite loads, and greater predator attraction at large colonies) there were no clear benefits. However sociable weavers do not seem to be limited in their choice of colony structure (only 48% of colony structures are inhabited: Chapter 4) so it is unlikely that birds are forced into coloniality by nest site limitation (Shields and Crook 1987; Robinson 1985; Post 1994). Therefore there may well be benefits of coloniality not addressed in the present study.

White et al. (1975) and Bartholomew et al. (1976) have shown that the nest mass of the sociable weaver provides insulation from the extremes of summer (31°C) and winter (-10 °C) temperatures. White et al. (1975) also reported a colony size effect. They found that chambers in a large colony were warmer than those in a smaller colony. The thermodynamic benefits of living in a large colony for non-breeding season survival (not measured in the present study) may be considerable. There are also other ways in which colonial living could increase survival. It is possible that during the non-breeding season when adult sociable weavers are reliant on seeds coloniality improves foraging efficiency (Ward and Zahavi 1973). Additionally flocking may provide protection from avian predators (the gabar gosshawk *Micronisus gabar* is an important predator of adult sociable weavers (Maclean 1973; pers. obs.). There may also be social benefits of coloniality such as co-operative nest building (chapter 2) or temperature conservation through huddling (Maclean 1973; Bartholomew et al. 1976) for sociable weavers. Additionally, in many species of cooperative breeder grown offspring delay dispersal when the benefits of philopatry outweigh the benefits of independent

breeding (Emlen 1991). If young sociable weavers are unlikely to be able to breed successfully elsewhere they may remain at home despite the costs of coloniality.

The absence of measurable benefits of coloniality in the present study may also be an artefact of the high environmental stochasticity at the study site (Appendix 1). There is likely to be variation in the costs and benefits of coloniality dependent upon the state of the environment; the results presented in this chapter represent the outcome of one of many possible environmental trajectories. Furthermore, to increase sample sizes, the indices were standardised for year effects meaning that any interactions between environment and colony size have been lost.

3.5.3 Conclusions

The data presented in this chapter do not explain the maintenance of coloniality in the sociable weaver. Although there was no net cost of coloniality (as measured by fledging success) three clear costs were determined: decreased foraging efficiency during the breeding season; increased adult ectoparasite loads; and increased nest predator attraction all seemed to correlate with large colony size. The current benefits of colonial living in the sociable weaver remain unclear.

CHAPTER 4: COLONIALITY AND SPATIAL STRUCTURE

4.1 INTRODUCTION

Breeding habitats are often spatially discrete habitable patches surrounded by an unsuitable matrix (Hewitt and Butlin 1997; Wiens 1997). As species use the environment at different scales the importance of this patchiness varies between species. For some species, despite the existence of discrete patches, inter-patch transfer of individuals is unrestricted and populations remain panmictic; while for others, inter-patch transfer of individuals is sufficiently limited that populations are spatially structured into systems of local sub-populations (Andrewartha and Birch 1954; den Boer 1968; Levins 1969; Hanski and Gilpin 1991; Hanski and Gilpin 1997). In these spatially structured species, migration between local populations influences local dynamics and may potentially lead to the colonization or recolonization of empty patches (Hanski and Simberloff 1997).

4.1.1 Forms of spatial structure

Studies of spatial population structure have largely focused on its consequences for genetics (Whitlock and McCauley 1990; Whitlock 1992; Whitlock 1994; Hedrick and Gilpin 1997) and conservation (Drechsler and Wissel 1998). Interest has centred on Levins' (1969) theoretically appealing concept of a metapopulation which is defined by Hanski and Simberloff (1997) as: "a large network of similar small patches [where migration from one local population to at least some other patches is possible], with local dynamics occurring at a much faster time scale than metapopulation dynamics"). However, Harrison (1994) and Harrison and Taylor (1997) point out that the classic Levins metapopulation represents just one of many possible forms of spatial structure. They stress the importance of the further investigation of these forms, suggesting that they can be valuably defined using two axes (Fig 4.1).

Harrison and Taylor's (1997) first axis is the degree of variance in population persistence between patches. This determines the variance in rate of local extinction between patches. If the relative persistence of populations in all patches in a network is similar, then regional persistence (the time until all the local populations have gone extinct) will be determined by the balance between extinction and recolonization across the entire network. However, if some populations in a system are much more persistent than others (for example, as a result of greater patch size or quality) then the dynamics of these populations alone will determine regional persistence. Networks with this property are often styled mainland-island

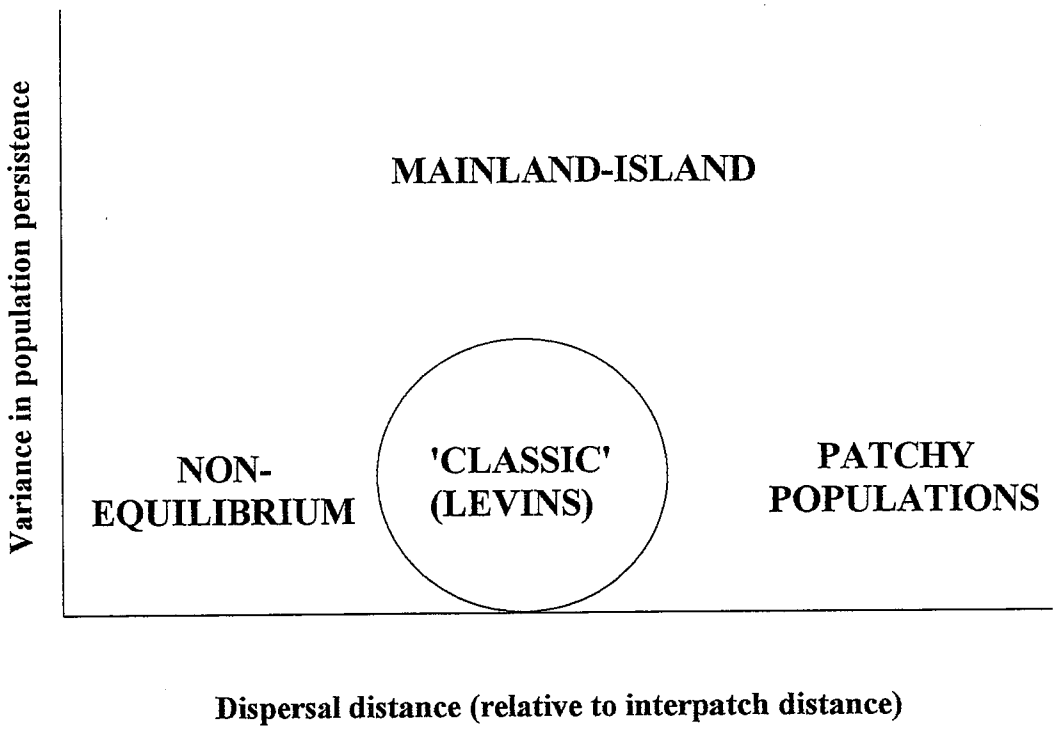


Fig 4.1 The type of spatial structure shown by a species is determined by the dispersal distance relative to the interpatch distance and by the degree of variance in population persistence - from Harrison and Taylor (1997).

populations (Fig 4.1). Harrison and Taylor's second axis is the dispersal distance relative to the inter-patch distance which determines the importance of spatial position for local colonization rate. When dispersal distance is high relative to interpatch distance, progeny from different patches will reassort each generation forming a demographically unified system (patchy population: Fig 4.1). As dispersal distance decreases relative to interpatch distance, migration becomes more limited and populations less demographically unified (Levins metapopulation: Fig 4.1). Finally, when dispersal distance is very low compared to interpatch distance transfers between patches do not occur (non-equilibrium metapopulation: Fig 4.1). Harrison and Taylor (1997) point out that a system may include several different forms of spatial structure (for example, a central patchy population surrounded by more isolated outlying patches). They conclude that a "great variety of spatial structure exists in natural populations" and urge researchers "to take fully into account the different types of spatial structure that are possible".

4.1.2 Investigating spatial population dynamics: patch models

In order to determine the form of spatial structure of a patch system information about the dynamics of local populations must be collected. The measurement of temporal variation in local population sizes over an entire patch system is often difficult, if not impossible (Lahaye et al. 1994; Spendelow et al. 1995). One alternative is the use of incidence (presence or absence) of populations in patches (Gilpin and Diamond 1976). This approach, developed for the investigation of Pacific island-bird communities, has been adapted for use in the investigation of metapopulation structures (Hanski 1994a,b, 1999; Hanski et al. 1994). Two patch-specific parameters describe patch dynamics: the probability of patch extinction (the reciprocal of the extinction rate); and the probability of patch colonization (the reciprocal of the colonization rate). These are in turn closely linked to the probability of patch occupancy. Using a linear first order Markov chain, the relationship between J_i the stationary probability of patch occupancy, C_i the patch specific probability of colonization and E_i, the patch specific probability of extinction can be estimated as (Hanski 1994b):

$$J_i = \frac{C_i}{C_i + E_i} \qquad (4.1)$$

If spatial structure has an important influence on local population dynamics then the stationary (time independent) transition probabilities of patches are predicted to be affected by patch characteristics. Three specific predictions are that: (1) The extinction rate E_i of a patch is determined by local population size (due to increased

extinction rates resulting from demographic stochasticity or loss of genetic variation in small patches (Shaffer 1981; Tracy and George 1992)). This prediction has gained support from studies in many patchily distributed species including: pikas *Ochotona princeps* living in discrete mine diggings (Smith 1980), several spiders living on Bahamian islands (Schoener and Spiller 1987), the European nuthatch *Sitta europaea* living in forest plots (Verboom et al. 1991), a tephritid fly *Urophura cardui* (Eber and Brandl 1996), and many butterfly species (Harrison et al. 1988; for reviews see Thomas and Hanski 1997; Hanski 1999). (2) The colonisation rate C_i of a patch will increase as a function of the number of potential immigrants arriving at the patch per unit time interval. Furthermore the spatial structure of the patch network (size, position and occupancy status of nearby patches) will determine the number of potential immigrants. Species in which this prediction has received empirical support include: pikas (Smith 1980), nuthatches (Verboom et al. 1991), the spotted skipper *Hesperia comma* living on grazed grassland (Thomas and Jones 1993) and the pool frog *Rana lessonae* (Sjogren 1991; Sjogren Gulve 1994). (3) At a first approximation (equation 4.1), the probability of patch occupancy is predicted to (i) increase with increasing patch specific colonisation probability (and hence increasing potential immigration) and (ii) decrease with increasing patch specific extinction rate (and hence decreasing population size). These two predictions have received support in at least 22 studies of patch occupancy (reviewed in Hanski 1999). Examples include butterflies such as the spotted skipper (Thomas and Jones 1993) and the bay checkerspot *Euphydryas editha bayensis* living on serpentine outcrops (Harrison et al. 1988), the wart biter bush cricket *Decticus verrucivorus,* (Hjermann and Ims 1996), European nuthatches (Verboom et al. 1991), the hazel grouse *Bonasia bonasia* (Åberg et al. 1995), pikas (Smith 1980; Smith and Gilpin 1997) and the dormouse *Muscardinus avellanarius* living in forest plots (Bright et al. 1994).

4.1.3 Spatial structure and sociable weaver populations

This chapter explores the consequences of coloniality for the local population dynamics of sociable weavers. Sociable weavers represent a good candidate species for a patch based study of population structure for three reasons. First, coloniality appears to impose some degree of spatial structure on sociable weavers populations. Sociable weaver colony structures are not strictly equivalent to the resource patches identified in most studies of spatial structure (e.g. forest fragments (Verboom et al. 1991), meadows (Hanski et al. 1995), pools (Sjogren Gulve 1994) or mine workings (Smith and Gilpin 1997) but like classic resource patches, colony structures are spatially discrete and provide important benefits to their inhabitants (for example, environmental amelioration (White et al. 1975)). Additionally, if

social divisions between colonies may further subdivide local populations (Stacey et al. (1997) suggest water voles *Arvicola terrestris* (Stodart 1970) and black-tailed prairie dogs *Cynomys ludovicianus* (Dobson et al. 1997) as examples of species in which spatial structure may result from social structure). Second, as dispersal distance (relative to inter-patch distance) is likely to be an important factor influencing spatial population structure it is noteworthy that inter-colony migration is reported to be rare in the sociable weaver (Maclean 1973). However, movement of individuals does not appear to be so limited as to prevent recolonization of empty colony structures (pers. obs.). Finally, the sociable weaver's colony systems are simple to survey; colony structures are semi-permanent, visually obvious and occupancy status is easy to determine.

It is important to draw a distinction between colony use, which was investigated in the present study and the causes of any underlying patterns in the colony size and/or position. Thus this chapter addresses the question 'Given the size and position of existing colony structures how do sociable weavers use them?' rather than, 'What determines the pattern size and position of colony structures?'

4.2 AIMS

The central aim of this chapter is to investigate the hypothesis that the spatial division of sociable weaver populations into colonies influences sociable weaver population dynamics. If coloniality does impose spatial structure, then the size and position of a colony are predicted to influence local dynamics. Three predictions were tested.

(1) Local (colony) extinction rate decreases with increasing colony size. Thus, the rate of extinction of small active colonies is predicted to be greater than that of large active colonies.

(2) Local (colony structure) colonization rate decreases with decreasing numbers of potential immigrants (i.e. increasing isolation). In other words, inactive colony structures which are close to active colonies are more likely to be colonized than isolated inactive structures.

(3) Based upon the combination of (i) and (ii) the stationary colony occupancy probability increases with increasing colony size and decreasing colony isolation. Thus, colony structures which are small and isolated are predicted to be less likely to be occupied by sociable weavers while those which are large and surrounded by active colonies are more likely to be occupied.

4.3 METHODS

4.3.1 Colony occupancy survey

During the austral autumns of 1997 and 1998 all colony structures (n = 283) in an area of approximately 8.5 km by 6 km (51 km^2) were surveyed at Claratal farm, Namibia (chapter 1). The area was surveyed on foot ensuring that all colony structures were recorded. Six variables were collected for each colony structure:

(i) Colony structure location was determined using a hand held Global Positioning System (GPS) unit (Garmin GPS 45XL). All positions were recorded to an accuracy of 0.0001 degrees latitude and 0.0001 degrees longitude (for all colony positions the GPS unit reported a horizontal accuracy of 40m or better). These co-ordinates were then transformed to a standard Cartesian grid.

(ii) Colony structure size was measured as the number of good chambers at a colony. The numbers of good chambers (i.e. structurally complete, occupiable, although not necessarily recently occupied, chambers) and poor chambers (i.e. partially complete) were recorded separately. In order to determine if there was a spatial pattern in colony size, spatial autocorrelation of colony size was investigated using Moran's I (program supplied by A. Brewer).

(iii) Colony structure occupancy was determined as active or inactive using: (a) the presence of adult or juvenile sociable weavers at the colony; (b) the presence or absence of fresh sociable weaver faeces under the colony nest masses; (c) evidence of recent nest building at the colony structure; (d) presence of roosting sociable weavers at night.

(iv) Three other general colony characteristics were recorded: (a) the number of nest masses composing the colony structure (chapter 1); (b) the tree species on which the colony structure was built; (c) the approximate height of the colony structure (ground level to the lower surface of the nestmass).

4.3.2 Colony size and population size

The relationship between **colony structure size** (Section 4.3.ii) and **population size** was investigated using linear regression of $\log_{10}$ transformed variables for 37 colonies at which mist netting was carried out. Sociable weaver **population size** was estimated based upon the number of mist-net captures

during ringing plus the number of birds observed to avoid the mist nets (in the region of 10% at most colonies).

4.3.3 Dispersal distance

Ringing recaptures (chapter 1) were used to assess the dispersal rates of sociable weavers both as fledglings and adults. The recapture records of all birds fledged from study colonies (i.e. those colonies at which all nestlings were ringed) in the austral summers of 1996 (n = 7 colonies) and 1997 (n = 7 colonies) were checked for natal and non-natal recapture. The recapture records of all adults caught at these colonies in the austral summers of 1996 and 1997 were also checked. These data along with additional recapture records for fledglings from colonies at which all chicks were not ringed (n = 1 recapture) were used to calculate mean dispersal distances.

As the observed pattern of recaptures is dependent upon sampling effort and location (Barrowclough 1978; Koenig et al. 1996) additional estimates of mean dispersal distance were calculated with a correction for sampling effort (Appendix 2).

4.3.4 Analysis of spatially structured population dynamics

(a) Estimation of population size and isolation

(i) The relationship determined between structural colony size and population size in Section 4.3.2 was used to estimate the potential adult population size of each colony structure.

(ii) Colony isolation (M_i number of potential immigrants) was estimated, assuming a negative exponential distribution of dispersal distances (Gilpin and Diamond 1976), as (Hanski 1994):

$$M_i = \sum_{k=1}^{n} j_k P_k \exp(-d_{ik}/D') \qquad (4.2)$$

where D' is the species specific dispersal constant (Gilpin and Diamond 1976; Harrison et al. 1988; Hanski et al. 1994), j_k is the occupancy status of colony k (1 for active, 0 for inactive), P_k is the estimated population size of colony k and d_{ik} is the distance between colonies i and k. As mean dispersal distance is difficult to measure M_i was calculated using three estimates of D' covering the range of estimated values (500m, 750m, 1000m; section 5.3.3; Appendix 2). All colonies (n = 283) were used in the calculation of isolation but to minimise boundary error

all colonies within 1km of the eastern, southern and western borders of the study area (n = 91; Figure 4.2) were excluded from further analyses. As there were few or no colonies in the area immediately beyond its northern border (due to a change in terrain) no northern edge colonies were excluded.

(b) Statistical analysis

Forward stepwise logistic regressions were used to analyse the influence of estimated population size, isolation and colony height on the probabilities of extinction, colonization and incidence within the studied sociable weaver colony system. The analyses were repeated using the three estimates of M_i (section 4.3.4; Appendix 2). All colonies with zero good chambers (n = 48) were judged to be currently incapable of supporting a population and were therefore excluded from subsequent analyses leaving 144 colonies in the final analyses.

The analysis of colonization compared colonies inactive in 1997 and subsequently active in 1998 with those inactive in both years. The analysis of extinction compared colonies active in 1997 and subsequently inactive in 1998 with those active in both years. The analysis of occupancy compared colonies active in 1998 with those inactive in 1998. Potential population size and isolation were normalized by log-transformation.

4.4 RESULTS

4.4.1 Colony survey

For the total study area (including edges) in both 1997 and 1998, 48% (136 of 283) of all colonies were active. Mean (± s.d.) colony size was 17.7 good chambers (± 20.6) (median = 11; Figure 4.3.a). Six forms of support structures were recorded (*Acacia erioloba* (70% , n = 199), *Ziziphus micronata* (17%, n = 48), dead trees (mostly *A. erioloba;* 10%, n = 29), an unidentified tree species (0.4%, n = 1) and man made structures (2%, n = 6); Figure 4.3.b). Mean colony height (± s.d.) was 3.35m (± 1.4, n = 280; Figure 4.3.c). There was no correlation between colony size (number of good chambers) and height (r_s = 0.08, n = 280).

There was no evidence of spatial autocorrelation in colony size (Moran's I: Bonferroni corrected $p > 0.05$ for the spatial autocorrelogram; n = 283 colonies, 10 distance classes) so colonies were not spatially clustered by size. Mean nearest neighbour distance was 160m. Mean distance to the nearest colony: with at least one chamber was 200m, with at least 10 chambers was 330m and with at least 30 chambers was 790m (n = 192 central colonies).

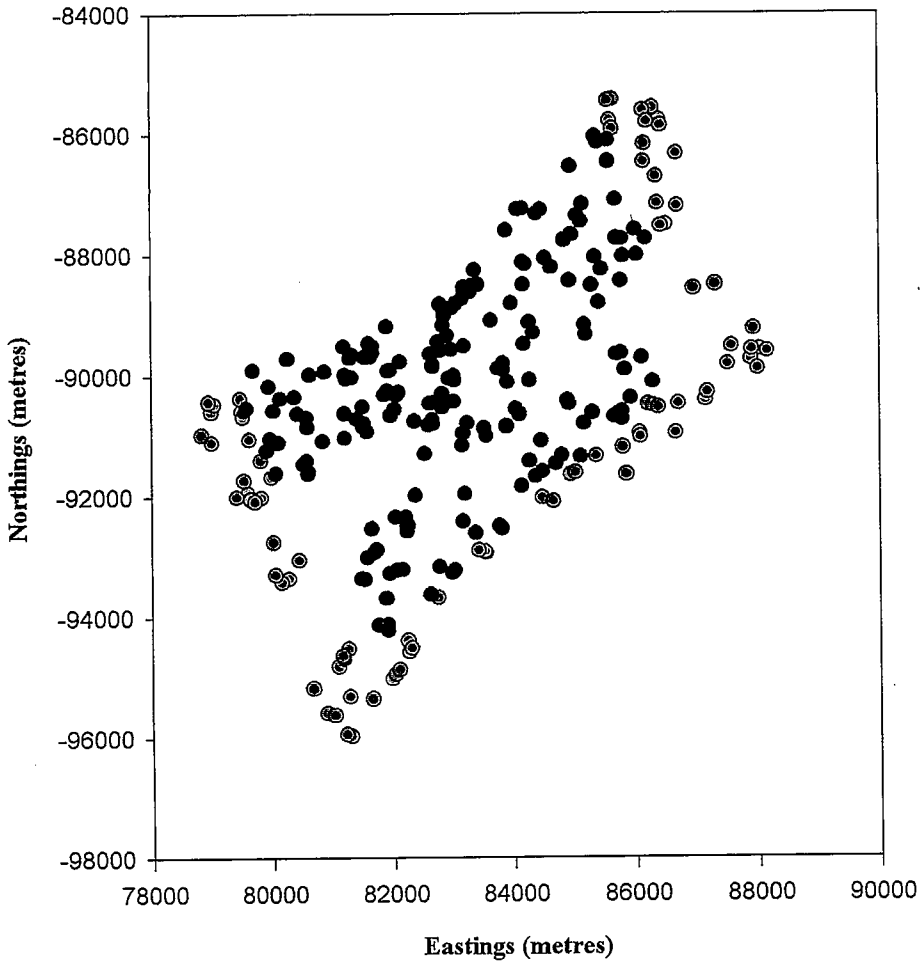


Figure 4.2 Spatial position of colonies at the Claratal study site. Green circles represent colonies inside a 1Km edge zone (to the E, S and W) excluded from the analysis of population dynamics. Black circles are those included in the analysis. Distances are metres North and East of the point 16.000^{o} E, 22.000^{o} S.

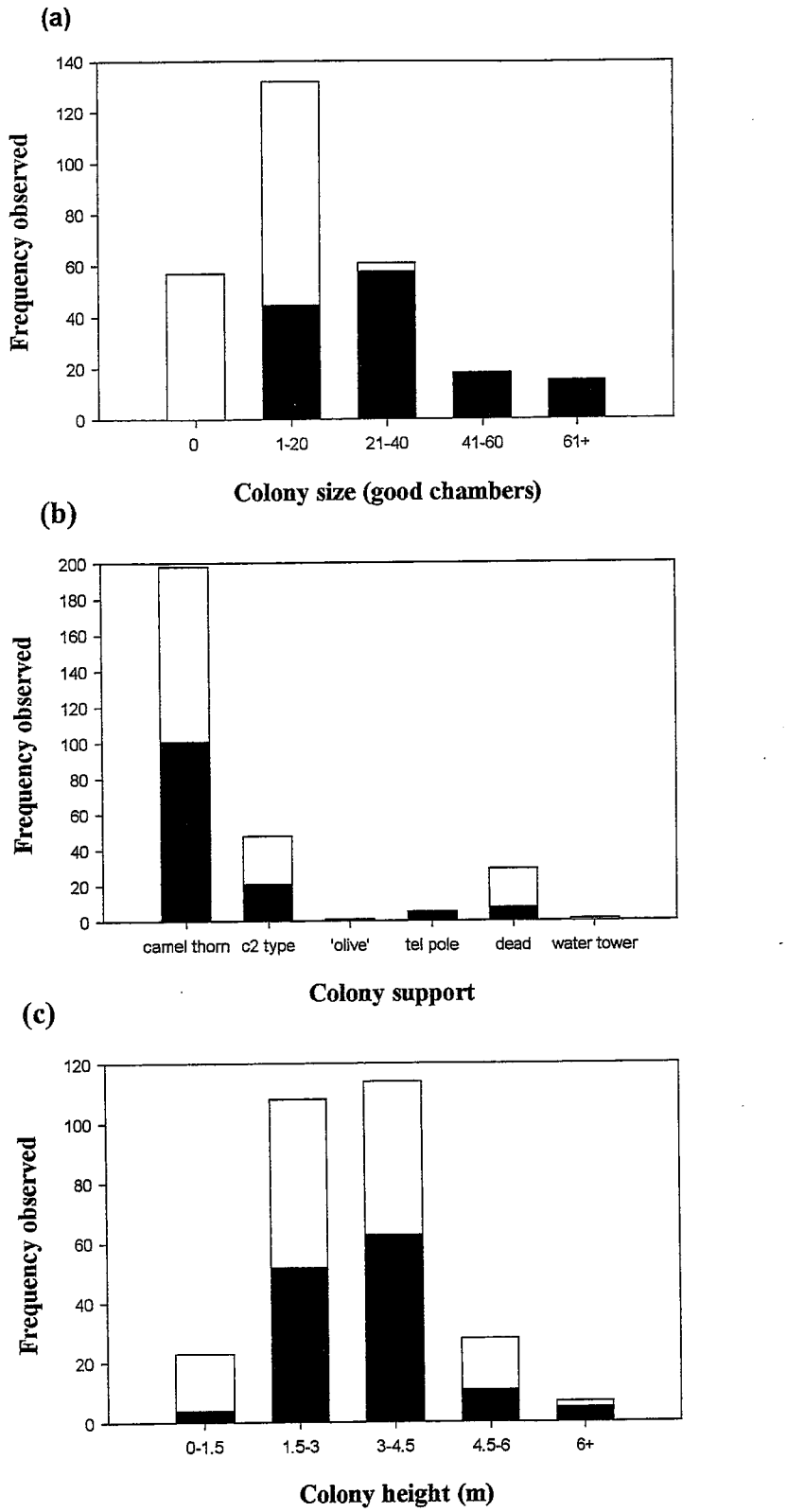


Figure 4.3. Frequency of colonies observed by: (a) Size class (mean size = 17.7 good chambers (s.e. = 1.22, median = 11 good chambers, n = 283).
(b) support structure and (c) height class (mean = 3.4 m, s.e. = 0.1, n = 280).
Filled bars represent active colonies, unfilled bars inactive colonies.

4.4.2 Colony size and population size

Colony size (good chambers) strongly predicts adult population size ($r^2 = 0.71$, n = 37, $p < 0.001$; Figure 4.4): population size = $0.425(\text{good chambers})^{1.06}$.

4.4.3 Dispersal distance

(a) Fledglings

None of the chicks ringed in 1996 and known to have fledged (n = 35) were recaptured in 1997 or 1998. Of the chicks known to have fledged in 1997 (n = 88), 30% (n = 26) were recaptured in 1998. Of those recaptured 77% (n = 20) were at their natal colony, while 23% (n = 6) had dispersed (Figure 4.5; Figure 4.6.a). The mean observed dispersal distance for 1997 to 1998 was 404 m (s.e.± 133, n = 27; Figure 4.6.b). The mean estimated dispersal distance for birds fledged in 1997, including a simple correction for the proportion of colonies at which a bird could have been recaptured (Appendix 2), was 864m (s.e. ± 136).

(b) Adults

Only 14% (17 out of 119) of adults captured in the breeding season of 1996 were recaptured in the breeding season of 1997. While 52% (49 out of 109) of adults captured in the 1997 breeding season were recaptured in 1998 (Figure 4.6.a). For the period 1997 to 1998, 86% (49 out of 57) of adults recaptured had not moved colony. The mean observed adult dispersal distance from 1997 to 1998 was 177m (s.e.± 59, n = 57; Figure 4.6.b). The mean estimated adult dispersal distance (period 1997 to 1998), including a simple correction for the proportion of colonies at which a bird could have been recaptured (Appendix 2), was 366m (s.e. ± 79).

All calculated dispersal distances are summarised in Table 4.1.

4.4.4 Analysis of local extinction, colonization and occupancy

(a) Local colonization

The mean colonization rate of unoccupied colony structures between 1997 and 1998 was 25% (15 of 60 colony structures inactive in 1997 were colonized by 1998: Figure 4.7). The results of a forward stepwise logistic regression with the colony parameters are reported in Table 4.2. Only log(potential population size) and a constant were included in the final model which was independent of the value of D' used (500m, 750m or 1000m). Thus estimated population size, but not isolation, had a significant effect on the probability of an empty colony being colonized. Testing the final model against the data used for parameterization, it correctly

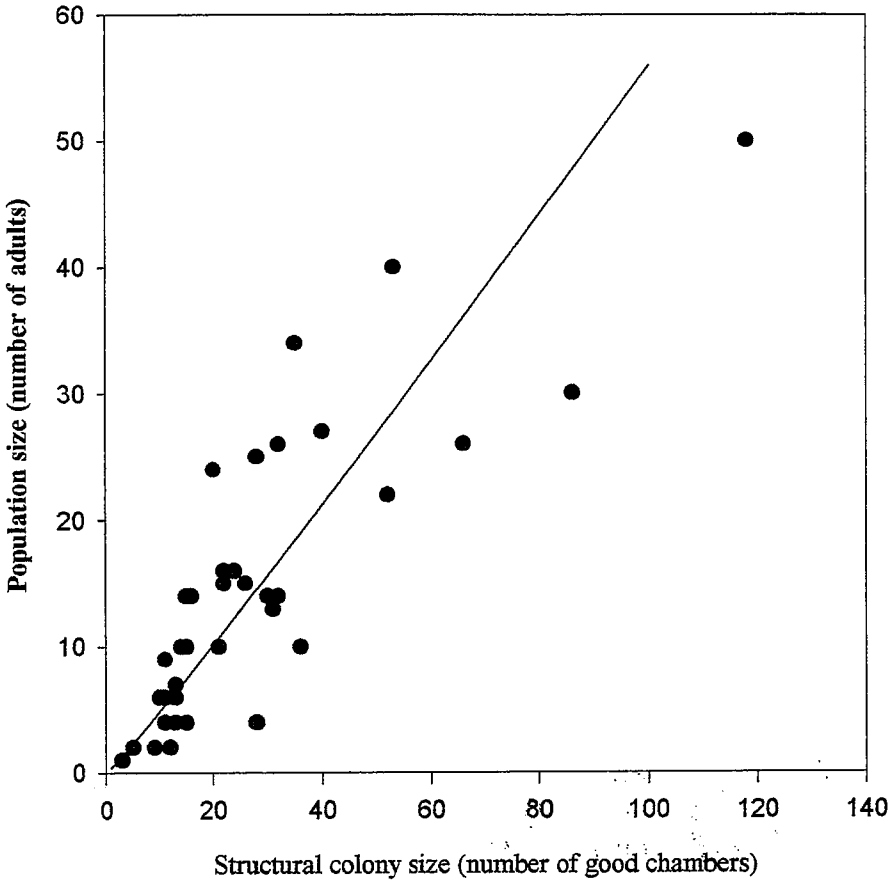


Figure 4.4 The relationship between structural colony size (number of good chambers) and population size (number of adults) for 37 sociable weaver colonies misted netted between 1995 and 1998. The line shows the fitted regression equation: log(adult population) = 1.06*log(good chambers) - 0.372, $r^2 = 0.719$, $n = 37$, $p < 0.001$).

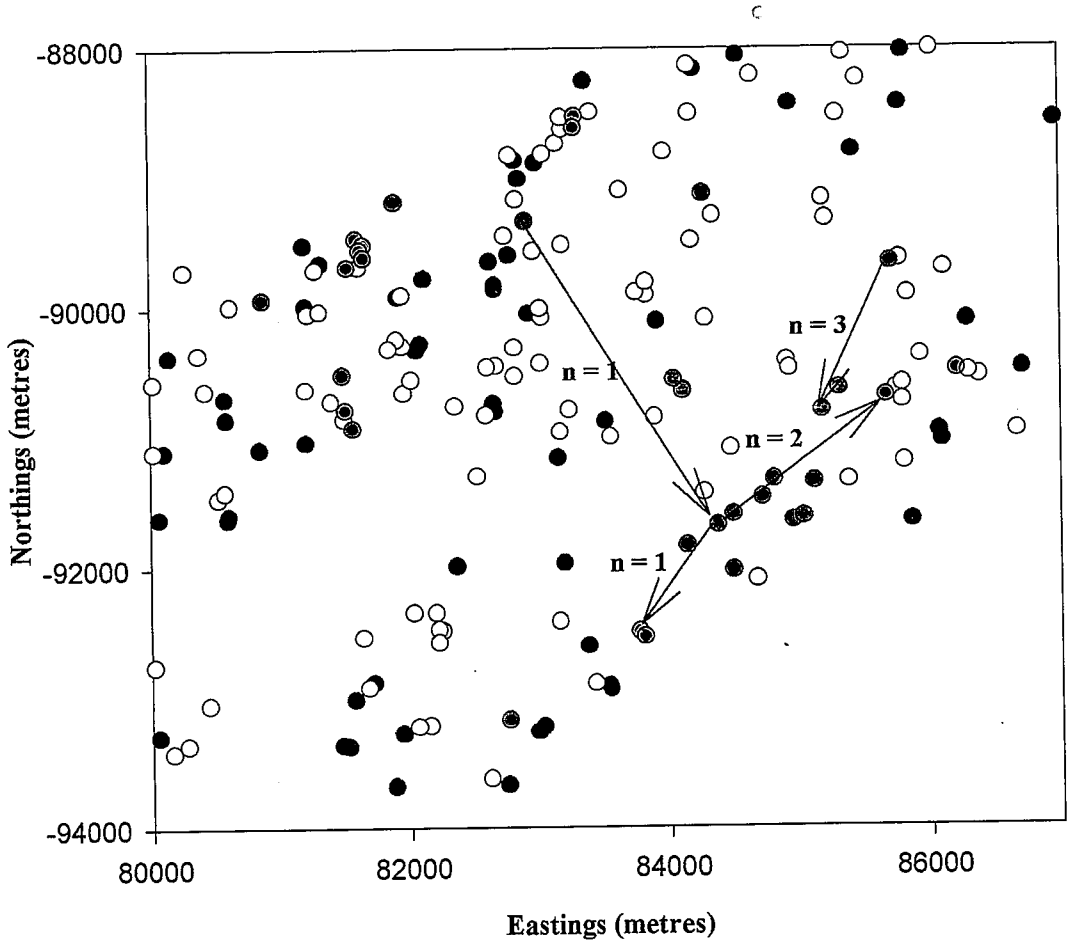


Figure 4.5 Spatial position of colonies at which mist netting took place during the study. Filled and empty black circles represent colonies active and inactive (in 1998) at which mist netting did not take place. Coloured circles represent colonies mist netted (if occupied) in all three years of the study (1995-98; blue), the second two years (1997-98; red) or the third year of the study (1998; green). Arrows show recorded natal dispersal (with number of birds).

Table 4.1 Dispersal distances for (a) observed recaptures and (b) estimates of potential recaptures correcting for recapture effort. Results are presented for fledglings, adults and all birds combined. Data for the period April 1997 to January 1998.

(a) Observed recaptures

Age class	mean (m)	n (recaptures)	SD
Fledglings	404	27	750
Adults	176	57	443
Combined	250	84	566

(b) Dispersal estimates correcting for recapture effort

Age class	mean (m)	n (estimated)	SD
Fledglings	864	44	905
Adults	466	88	684
Combined	614	118	794

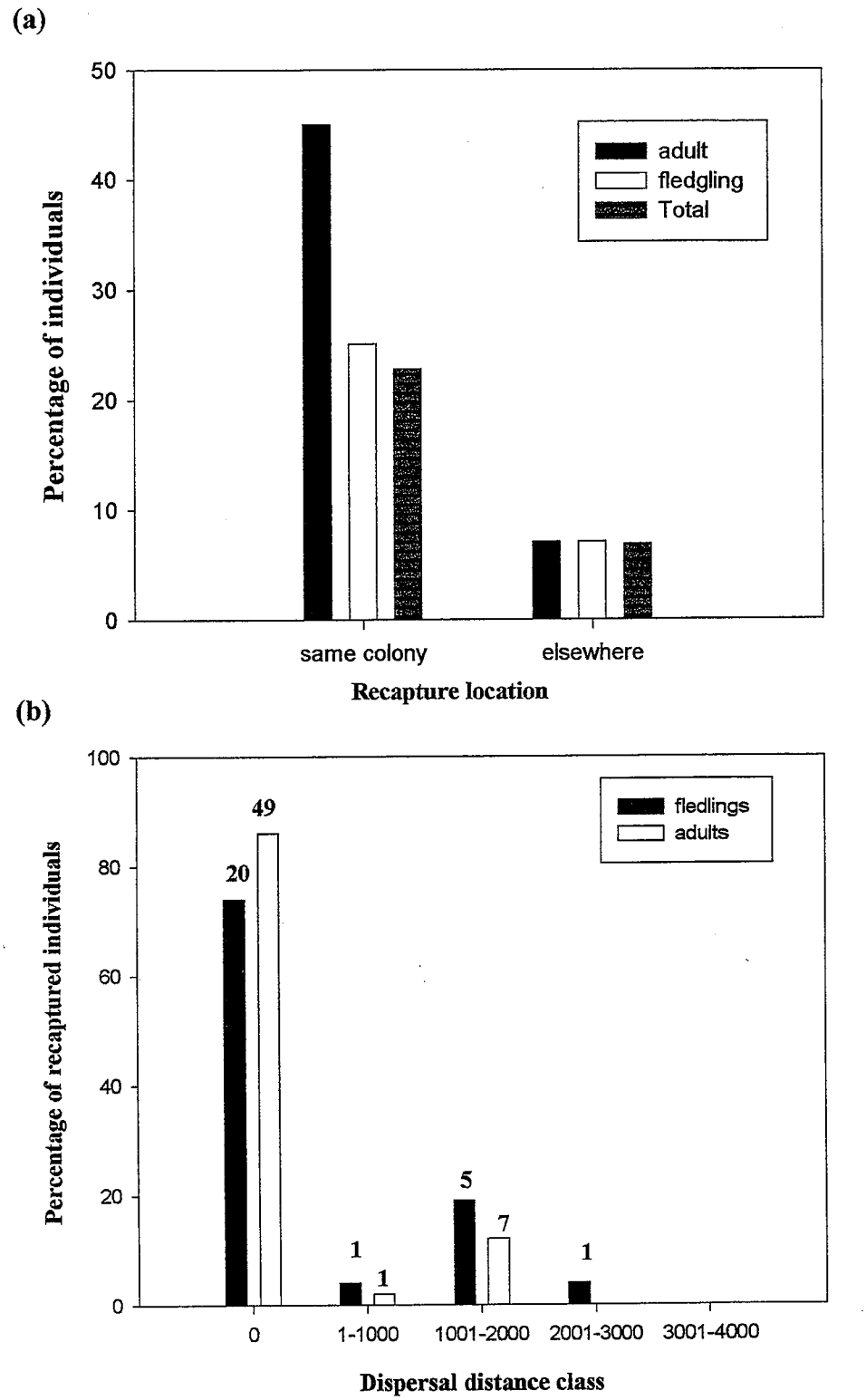


Fig 4.6.(a) Percentages of individuals (total n = 197) captured in 1997 which were recaptured at the same (fledglings: 20 out of 88; adults: 49 out of 109) and different colonies (fledglings: 6 out of 88; adults: 8 out of 109). (b) Percentage of all 1997-98 recaptures as a function of distance from natal colony. Mean (+/- s.e.) dispersal distance was 250m (+/- 62) (for adults, 176m (+/- 58.7); for fledglings, 404m (+/- 144)).

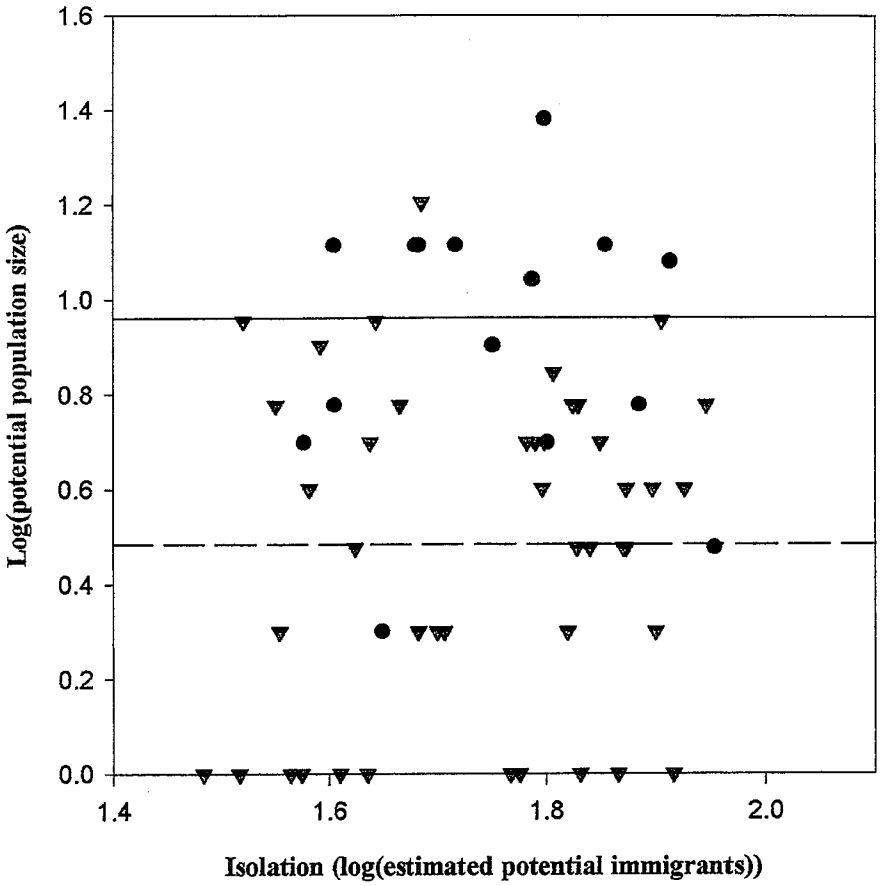


Figure 4.7 Potential population sizes, isolations (calculated D' = 500m) and local colonizations (red inverted triangles indicate colonies inactive in 1997 and 1998, black circles colonies inactive in 1997 but active in 1998) at the Claratal study site. Potential population size but not isolation had a significant effect on the probability of local colonization (logistic regression: Table 5.2). The solid and dashed lines show the calculated $c_i = 0.5$ and $c_i = 0.1$ probabilities from the regression.

Table 4.2. Results of a foward stepwise logistic regression of colonized versus non-colonized (1997/98) sociable weaver colony structures with potential population size, isolation and colony height. Population size and isolation were both log normalized. The final model was not influenced by the value of D' (results are presented for D' = 500m) used in the calculation of isolation.

Variable	Parameter estimate	SE	Wald value	df	p
Constant (final)	-4.431	1.206	13.49	1	0.0002
Population size	4.602	1.426	10.42	1	0.0012

Isolation (Wald score = 0.4524, df = 1, p = 0.50) and colony height (Wald score = 2.322, df = 1, p =0.13) did not enter the final model. Model chi^2 = 17.83, df = 1, $p < 0.0001$.

predicted colonization/continued-inactivity for 87% of colony structures. Of the 45 colonies which were not colonized between 1997 and 1998 the prediction of the final model was correct in 44 cases (98%). While in the case of the 15 colonies which were colonized, the prediction of the model was correct in eight (53%) cases.

(b) Local extinction

The mean extinction rate of occupied colony structures between 1997 and 1998 was 20% (14 of 70 colony structures active in 1997 were inactive in 1998: Figure 4.8). The results of a forward stepwise logistic regression with the colony parameters are reported in Table 4.3. Only log(potential population size) and a constant were included in the final model which was independent of the value of D' used (500m, 750m or 1000m). Thus, estimated population size but not isolation had a significant effect on the probability of an active colony becoming extinct. Testing the final model against the data used for parameterization, it correctly predicted extinction/persistence for 86% of colony structures. Of the 70 colonies which remained active from 1997 to 1998 the prediction of the model was correct in 69 cases (99%). However, in the case of the 14 colony structures which became inactive the model correctly predicted extinction in only 3 (21%) cases.

(c) Occupancy

The mean occupancy rate in 1998 was 59% (85 active colonies out of 144: Figure 4.9). The results of a forward stepwise logistic regression with the colony parameters are reported in Table 4.4. When D' was estimated as 500m, log(potential population size), log(isolation) and a constant were included in the final model (Table 4.4.a; Figure 4.9). However, when D' was estimated as 750m or 1000m only log(potential population size) and a constant were included in the final model (Table 4.4.b,c; Figures 4.10,4.11). Thus, if mean dispersal distance was estimated as a low value both colony size and isolation were found to have a significant effect on the probability of colony occupancy but with a slightly higher estimate of mean dispersal distance only colony size had a significant effect on the probability of colony occupancy. Using D' = 500m the model correctly classified occupancy status for 80% of colony structures when tested against the original data. Of the 59 unoccupied colony structures 43 (73%) were correctly classified. Of the 85 occupied colony structures 72 (85%) were correctly classified. Using D' = 750m or D' = 1000m the model was slightly less successful. It correctly classified occupancy status for 79% of colonies when tested against the original data. Of the 59 unoccupied colony structures, 40 (68%) were correctly classified. Of the 85 occupied colony structures 74 (87%) were correctly classified.

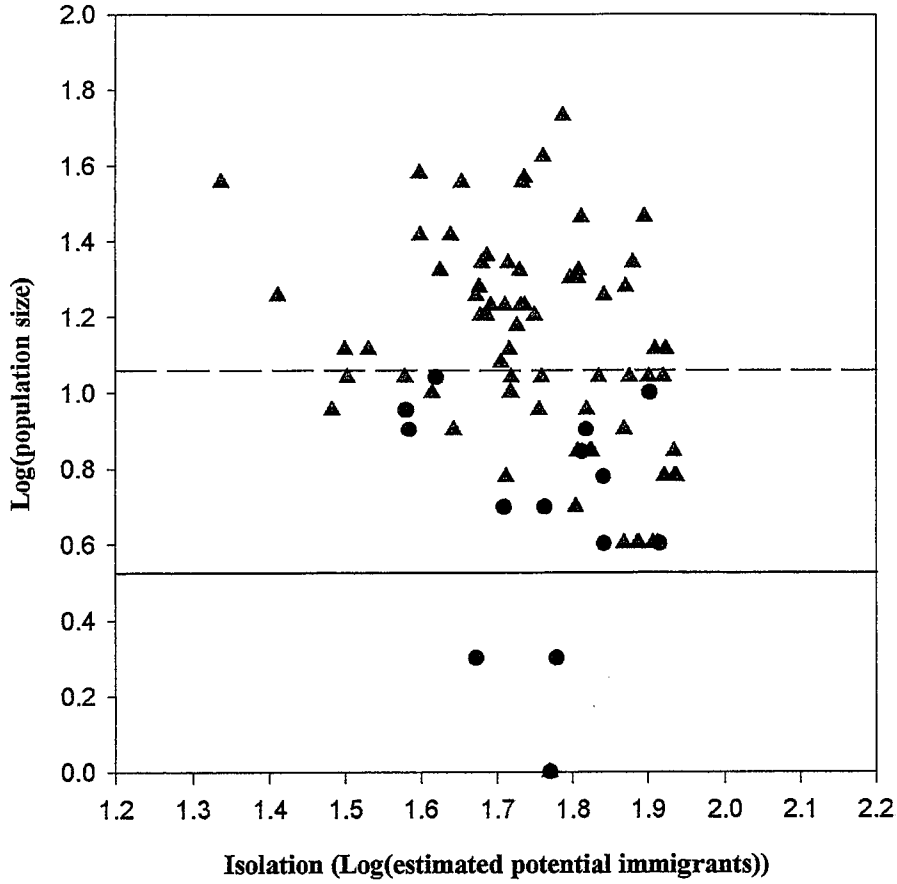


Fig. 4.8. Population sizes, isolations (calculated assuming D' = 500m) and local extinctions (blue triangles indicate colonies active in both 1997 and 1998, black circles colonies active in 1997 but not 1998) at the Claratal study site. Colony size but not isolation had a significant effect on the probability of local extinction (logistic regression: table 5.3). The solid and dashed lines shows the calculated $e_i = 0.5$ and $e_i = 0.1$ extinction probabilities from the regression.

Table 4.3. Results of a foward stepwise logistic regression of extinct versus persistent (1997/98) sociable weaver colony structures with population size, isolation and colony height. Population size and isolation were both log normalized. The final model was not influenced by the value of D' (results are presented for D' = 500m) used in the calculation of isolation.

Variable	Parameter estimate	SE	Wald value	df	p
Constant (final)	2.159	1.063	4.12	1	0.0424
Population size	-4.103	1.192	11.86	1	0.0006

Isolation (Wald score = 1.60, df = 1, p = 0.21) and colony height (Wald score = 0.03, df = 1, p = 0.87) did not enter the final model. Model chi^2 = 18.07, df = 1, $p < 0.0001$.

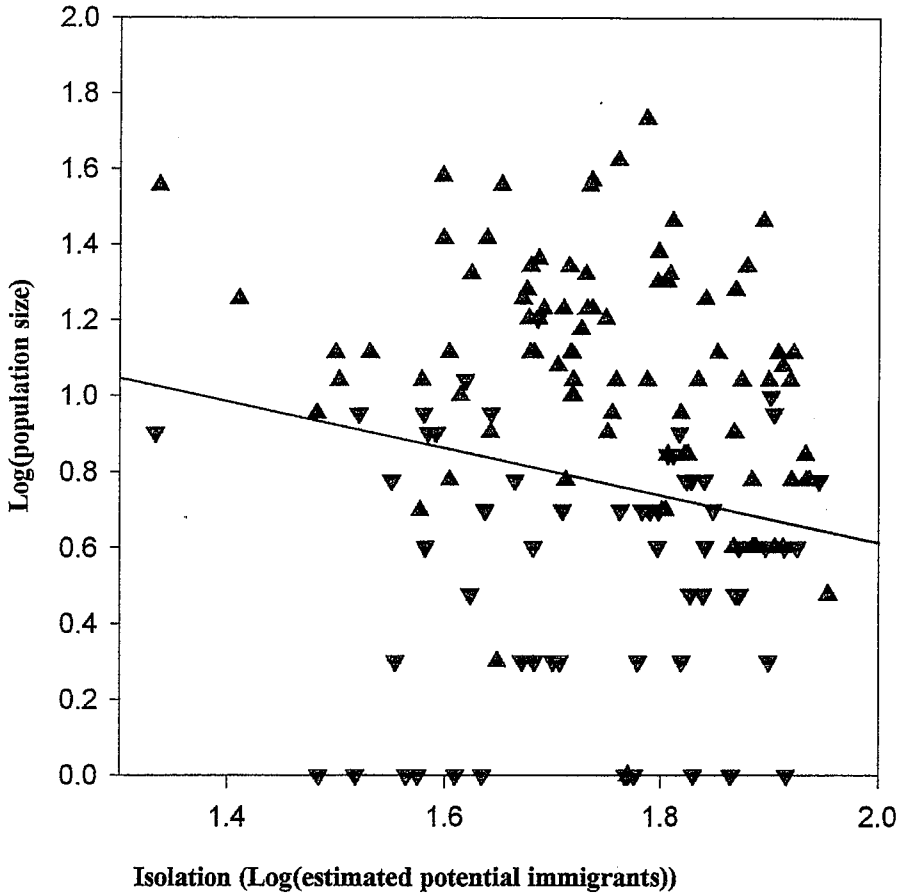


Figure 4.9 Population sizes, isolations (calculated assuming D' = 500m) and 1998 occupancies (blue triangles indicate occupied colonies, red inverted triangles unoccupied ones) at the Claratal study site. Both population size and isolation had a significant effect on the probability of colony occupancy (logistic regression: table 5.4.a). The line shows the calculated $J_i = 0.5$ incidence line; that it the line on which the probability of colony structures being occupied is 0.5..

Table 4.4. Results of a foward stepwise logistic regression of occupied versus un-occupied (1997/98) sociable weaver colony structures with population size, isolation and colony height. Population size and isolation were both log normalized. The final model was influenced by the value of D' used in the calculation of isolation. Results are presented for (a) D' = 500m, (b) D' = 750m (c) D' = 1000m.

(a) D' = 500m

Variable	Parameter estimate	SE	Wald value	df	p
Constant (final)	-10.558	3.553	8.83	1	0.003
Population size	5.702	1.007	32.06	1	0.0001
Isolation	3.527	1.792	3.87	1	0.049

Colony height (Wald score = 0.42, df =1, p = 0.52) did not enter the final model. Model chi^2 = 76.41, df = 1, $p < 0.0001$.

(b) D' = 750m

Variable	Parameter estimate	SE	Wald value	df	p
Constant (final)	-3.898	0.760	26.33	1	0.0001
Population size	5.145	0.879	34.26	1	0.0001

Colony height (Wald score = 0.54, df = 1, p = 0.46) and isolation (Wald score = 3.02, df = 1, p = 0.08) did not enter the final model. Model chi^2 = 72.364, df = 1, $p < 0.0001$.

(c) D' = 1000m

Variable	Parameter estimate	SE	Wald value	df	p
Constant (final)	-3.898	0.760	26.33	1	0.0001
Population size	5.145	0.879	34.26	1	0.0001

Colony height (Wald score = 0.54, df = 1, p = 0.46) and isolation (Wald score = 1.67, df = 1, p = 0.20) did not enter the final model. Model $chi^2 = 72.364$, df = 1, $p < 0.0001$.

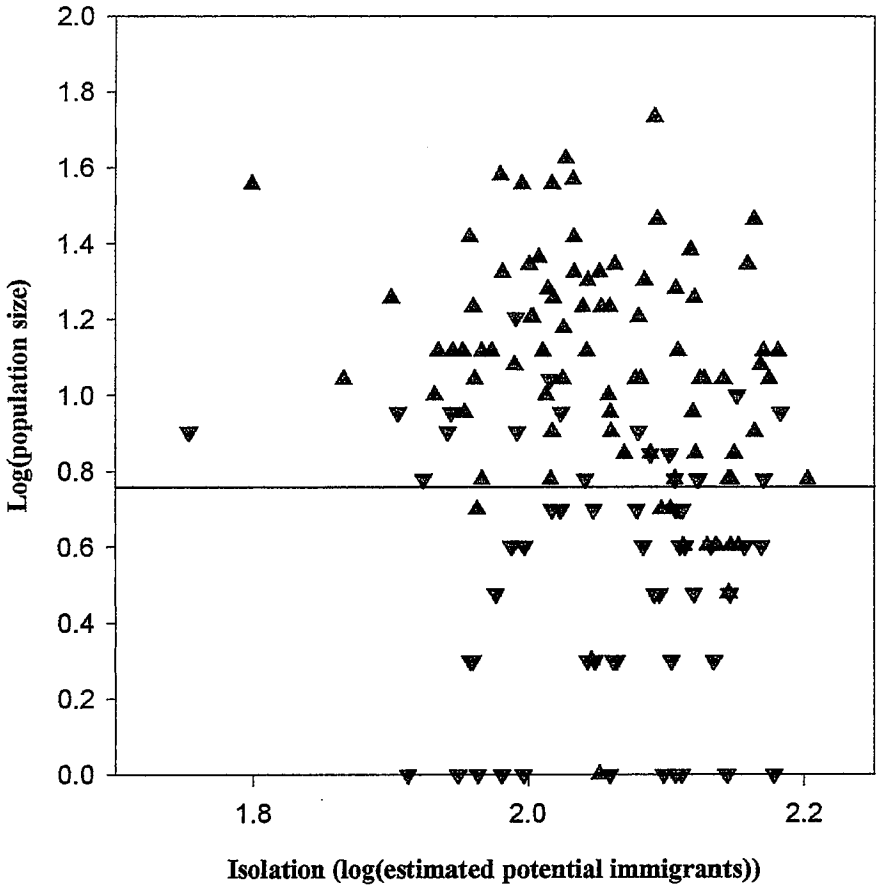


Figure 4.10 Population sizes, isolations (calculated assuming D' = 750m) and 1998 occupancies (blue triangles indicate occupied colonies, red inverted triangles unoccupied ones) at theClaratal study site. Population size but not isolation had a significant effect on the probability of colony occupancy (logistic regression: table 5.4.b). The line shows the calculated $J_i = 0.5$ incidence line (see Fig 4.9).

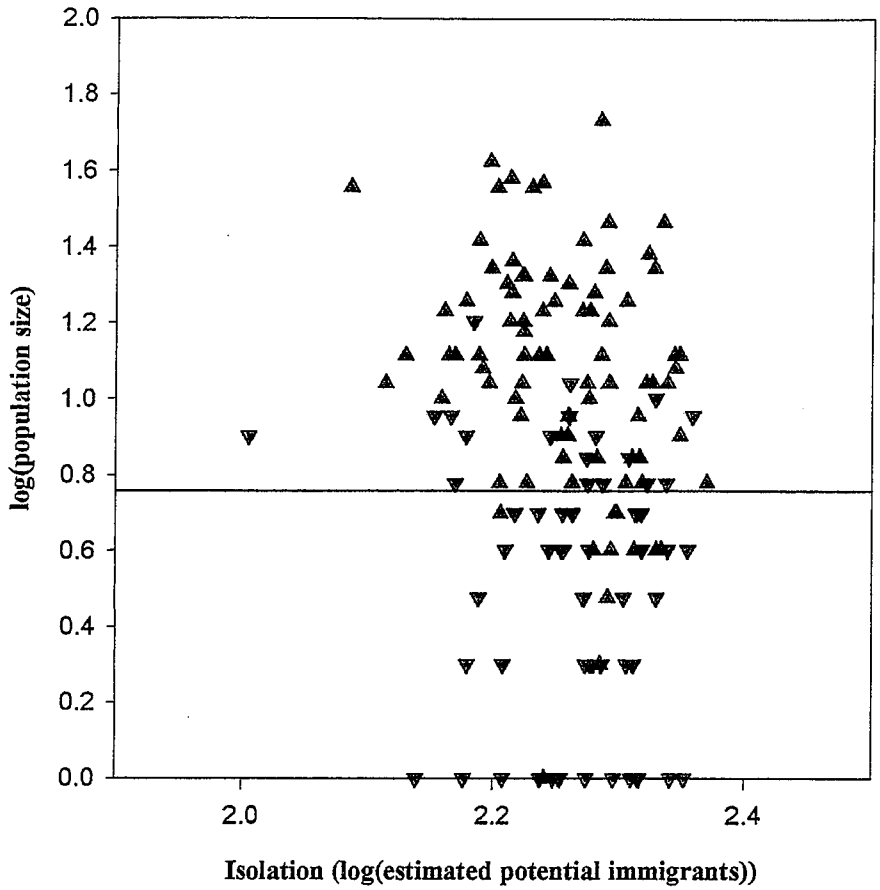


Figure 4.11. Population sizes, isolations (calculated assuming D' = 1000m) and 1998 occupancies (blue triangles indicate occupied colonies, red inverted triangles unoccupied ones) at the Claratal study site. Population size but not isolation had a significant effect on the probability of colony occupancy (logistic regression: table 5.4.c). The line shows the calculated $J_i = 0.5$ incidence line (see Fig 4.9).

4.5 DISCUSSION

Three main results are presented in this chapter. (1) The degree of isolation of an inactive colony structure did not effect the probability that it was colonized. However, size did effect the probability that an inactive structure was colonized; larger structures were more likely to become active than small ones. (2) Small, active colonies were more likely to undergo local-extinction than large ones but the degree of isolation of an active colony had no effect on its extinction probability. (3) Both potential population size and degree of isolation had significant effects on the probability of colony occupancy; larger colony structures were more likely to be occupied than small ones, and for low estimates of mean dispersal, less isolated colonies were more likely to be occupied than more isolated ones.

4.5.1 Colonization and extinction probabilities

Although the colonization probability of a patch is expected to depend upon its isolation (Hanski 1994b) the degree of isolation of inactive colony structures had no effect on colonization probability in the present study. This suggests that for sociable weavers the frequency (and distance) of dispersal between colonies does not limit colonization (Harrison and Taylor 1997). Interestingly, although colony size was not expected to influence colonization probability larger inactive colonies were more likely to be colonized than smaller ones. Similar patterns have been reported for *Hesperia comma* colonizing areas of grazed calcareous grassland (Thomas and Jones 1993) and *Urophura cardui* colonizing clumps of creeping thistles (Eber and Brandl 1996). Eber and Brandl (1996) suggest that dispersing individuals are more likely to randomly find larger habitat patches. In the case of the sociable weaver, large colonies may be more conspicuous to dispersers. Alternatively, they may offer greater benefits (White et. al. 1975; Bartholomew et. al. 1976), or be favoured as a result of the social dynamics of dispersal.

As expected, the extinction probability of sociable weaver colonies decreased with increasing colony size. It is noteworthy that, when tested against the original data, the final model (including constant and colony size alone) correctly predicted persistence for 99% of the colony structures which remained active but only predicted extinction for 21% of the colonies which became inactive. The reasons for this disparity can be clarified by considering the predictions of the final model shown graphically in Figure 4.8. While colonies with a population size greater than 11 were unlikely to go extinct ($e_i < 0.1$), and colonies with a very small population size (≤ 4 chambers) were likely to go extinct ($e_i > 0.5$), the pattern of

extinction for intermediate sized colonies (5-11 chambers) was not explained by population size alone. Thus it seems likely that several other factors are also important in local extinctions. These may include demographic stochasticity (Foley 1997), colony support tree collapses, genetic impoverishment (Saccheri et al. 1998), high local emigration (Kuussaari et al. 1996), or stochastic local variation in rates of predation, parasitism (Eber and Brandl 1996; Foley 1997; chapter 3), or resource availability (Lahaye et al. 1994; chapter 1). There was no significant effect of isolation on extinction probability so the results presented in this chapter do not support the existence of a rescue effect (i.e. of immigration saving 'doomed' patch from extinction - as has been reported for pikas and pool frogs (Smith 1980; Sjogren 1991, 1994; Hanski 1994)) in the sociable weaver.

4.5.2 Colony occupancy

In the present study there was a reduced probability of colony structure occupancy with decreasing colony structure size. Using a low estimate of dispersal (500m) to calculate isolation there was also a reduced probability of colony structure occupancy with increasing colony structure isolation. Although a similar pattern has been reported for some other birds (Verboom et al. 1991; Åberg et al. 1995), it means that, in the present study, the pattern of colony occupancy cannot be immediately reconciled with the patterns of colonization and extinction; although neither of the transition probabilities showed a significant effect of isolation, the pattern of colony occupancy was consistent (using the low dispersal estimate) with an effect of isolation on occupancy. However, colonization and extinction probabilities are, in general, likely to be sensitive to short term environmental variation so transition probabilities calculated during a short study may not accurately represent long term patterns (Eber and Brandl 1994,1996; Hanski 1997). For example, environmental variation, acting through reproductive success may influence both extinction rates and the number of potential dispersers - hence colonization rates. In the context of this study, rainfall at Claratal is highly variable (Chapter 1) and appears to influence sociable weaver reproductive success (Appendix 1) so that while the 1996 breeding season was poor with no fledglings recaptured as adults (either in their natal colonies or elsewhere) in 1997 the sociable weavers prospered with at least 30% of 1997 fledglings recruited into the 1998 adult population. This suggests that the difference between colonization and occupancy probabilities with respect to the effect of isolation may simply reflect high annual stochasticity in transition probabilities. In other words, it is possible that in any one year the effect of isolation on colonization or extinction probabilities is outweighed by environmental components but over many years an aggregate isolation effect generates the observed pattern of occupancies. It is also possible

that the relationship between occupancy and isolation is not mediated through dispersal. Other potential explanations include: (i) Local resource effects; if some areas of the study site are particularly productive then they may contain high densities of birds concurrent with a high level of colony occupancy. A similar argument could apply to the avoidance of patches of high local predator abundance. (ii) Social effects; there may be social advantages to living in areas with a high density of birds and high rates of colony occupancy (e.g. predator swamping during the breeding season).

Why is there an increase in the probability of occupancy with decreasing isolation? The hypothesis that colonization or rescue effect probabilities are greater for more connected patches because dispersers arrive more frequently (Hanski 1994) could explain this pattern. In that case more connected colony structures should be colonized more frequently yet they were not.

4.5.3 Coloniality and local population dynamics in the sociable weaver

Does coloniality influence local population dynamics in the sociable weaver? Sociable weaver colonies vary in size and position. In this study colony size had a clear effect on local population dynamics. Larger colonies were more likely to be occupied, more likely to be colonized if unoccupied and less likely to become extinct when they were occupied than small colonies. The effect of colony isolation on local dynamics was less clear cut. The difficulty in measuring dispersal and in particular occasional long distance dispersal (Barrowclough 1978; Edwards 1993a; Koenig et al. 1996), combined with uncertainty over the form of the expected distribution of dispersal distances (Harrison et al. 1988) created methodologically problems which made it difficult to determine the effect of colony position on local population dynamics.

In order to clarify the effect of changing mean dispersal distance (D') for the outcome of the model, several values were used. The outcome of the analysis of colony occupancy was sensitive to the value of D used; the effect of isolation on occupancy was only significant when the estimated mean dispersal distance used was 500m. As explained above (section 4.5.2), without further work the biological significance of this result is difficult to establish. A priority for future work will be to investigate patterns of temporal variation in the transition probabilities and to investigate the relationship between long and short-term patterns of transition probabilities and occupancy. It would also be valuable to

assess the importance of dispersal and non-dispersal mediated explanations for the lower frequency of occupancy at more isolated colonies.

Another important area for future research is the patterns of behaviour underlying local population dynamics. Individuals need not die for patches to undergo local-extinction; they simply need to move (Kuussaari et al 1996). In the sociable weaver there is anecdotal evidence that whole colonies re-locate. Maclean (1973) described a group of sociable weavers arriving at a formerly abandoned nest mass, roosting there for some time, and then suddenly leaving. In addition, during the course of the present study, the birds roosting at colony 15 moved together to colony 12 between the 1997 and 1998 field seasons (see page 62). These observations suggest that social system and the behavioural dynamics of dispersal cannot be ignored in the investigation of spatial structure in the sociable weaver and hence that the behavioural details of colonization and extinction events deserve investigation.

4.5.4 Conclusions

This chapter presents evidence that colony size (and possibly position) influence local population dynamics and patterns of colony occupancy in the sociable weaver. However, the lack of association between colony isolation and colonization probability suggests that the lower probability of occupancy for more isolated colonies may be correlational rather than causal. Further detailed data are needed on the behavioural dynamics of colonizations and extinctions and on environmental variation in dispersal, occupancy and the transition probabilities in the sociable weaver.

CHAPTER 5: COLONIALITY AND GENETIC STRUCTURE

5.1 INTRODUCTION

The frequency and distribution of genotypes within a population has important implications for evolutionary processes (Hewitt and Butlin 1997) and in particular the evolution of altruistic behaviours (Hamilton 1964a,b; Bourke 1997). Therefore the genetic structure of a species is of fundamental evolutionary importance. Many factors are expected to influence this structure. Three of the most important are: (i) a species' pattern of social dispersion; (ii) its patterns of dispersal; and (iii) the genetic outcome of its mating system.

5.1.1 Why study genetic structure?

Three consequences of a species' genetic structure which have attracted particular attention are: (i) the evolutionary implications of the differentiation of isolated or partially isolated local populations for the occurrence of local adaptation (Pope 1992; Dias and Blondel 1996; Hewitt and Butlin 1997; Martinez et al. 1999) or speciation (Shwartz and Armitage 1980; Baker et al. 1995); (ii) the importance of understanding genetic structure for successful maintenance of genetic diversity during conservation attempts (Sugg et al. 1996); and (iii) the potential for the evolution of kin selected altruistic behaviours when social interactions occur between related individuals (Hamilton 1964a). This study concentrates on the last of these.

Hamilton (1964a) showed that a gene for altruistic behaviour will undergo selection when,

$$rb - c > 0 \qquad (5.1)$$

where r is the altruist's relatedness to the beneficiary, b is the fitness benefit gained by the beneficiary and c is the fitness cost paid by altruist; "no one is prepared to sacrifice his life for any single person, but everyone will sacrifice it when he can thereby save more than two brothers or four half brothers or eight first cousins..." (Hamilton 1964a, p16). Hamilton's rule (1964a,b) has formed the basis for much evolutionary analysis of sociality. It has gained particular support from detailed studies of cooperation and conflict in cooperative breeders (occurrence of allo-parental care: Bourke 1997; Emlen 1997; patterns of care: Emlen and Wrege 1988; Curry 1988; Russell 1999; conflict over reproductive skew: Keller and Reeve 1994; Jamieson et al. 1994; offspring sex ratios in social hymenoptera: Trivers and Hare

1976). While it is important to note that kin selection is not the only potential route to altruism (Trivers 1971; Jamieson and Craig 1987; Wilkinson 1992; Zahavi 1995; Dugatkin 1997) studies of cooperative breeding and other altruistic behaviours emphasise the close relationship between genetic structure and patterns of social behaviour (Sherman 1977; Holmes and Sherman 1982; Wilkinson 1984,1985a, 1992; Packer et al 1991; Gomper et al. 1997).

5.1.2 Factors influencing genetic structure

Most work on genetic structure has concentrated on the existence of local, partially isolated breeding groups, demes (Wright 1965; Fleischer 1983). However, several recent theoretical (Chesser 1991a,b; Chesser et al. 1993; Sugg and Chesser 1994; De Jong et al. 1994) and empirical studies (Pope 1992; De Ruiter et al. 1994; Dobson et al. 1997) have focused on genetic structure within social groups. Chesser's (1991a) approach is based on the sub-division of classical demes into social lineages; family groups maintained by the fidelity of related individuals. He has suggested that several aspects of behaviour will influence the patterns of coancestry between and inbreeding within individuals of a species.

Perhaps the most important factor in the determination of genetic structure is social structure, including the demographic make up of social groups and the patterns of dispersal between them. When populations are divided into small isolated sub-populations and dispersal is limited, genetic divergence as a result of drift is likely to occur (Hedrick 1985; Baker et al. 1995). However, genetic structure may also develop if dispersal from social groups is asymmetrical with respect to sex; when only one sex remains philopatric high levels of coancestry may accrue within social lineages (Chesser 1991a). Several empirical studies have demonstrated this pattern of high relatedness between individuals of the philopatric sex (chimpanzees *Pan troglodytes:* Morin et al. 1994; European rabbits *Oryctolagus cuniculus:* Webb et al. 1995; savannah baboons *Papio cyanocephalus:* Altmann et al. 1996; white nosed coatis *Nasua narica:* Gompper et al. 1998; long-tailed macaques *Macaca fasicularis:* De Ruiter and Geffen 1998) or have found a difference between the sexes on the basis of a genetic assignment index (Favre et al. 1997) or minisatellite fingerprint similarity (Lehman et al. 1992). However, when individuals disperse with relatives (De Ruiter and Geffen 1998) or disperse to be with relatives (Girman et al. 1997) relatedness between members of the dispersing sex may also be high. In African wild dogs *Lycaon pictus* neither sex is philopatric, instead individuals disperse as same sex sibling groups thus forming packs with high intra- but low inter-sex adult relatedness (Girman et al. 1997).

The mating system of a species is also expected to influence genetic structure; variances in male and female reproductive success will determine the probability of shared paternity or maternity and hence coefficients of coancestry between offspring (Chesser 1991a,b; Sugg and Chesser 1994). Genetic structuring is expected to increase with decreasing numbers of breeding females per lineage (De Ruiter and Geffen's (1998) description of higher relatedness in smaller matrilines in the long tailed macaque provides support for this prediction). Genetic structure should also increase as a result of high reproductive skew (Chesser 1991a,b). If reproductive success is skewed towards a small subset of males either as a result of social polygyny or extra-pair copulation (Mulder at al. 1994) then average relatedness in offspring across broods may increase. However, despite the 46% mean maximum paternity gained by top males at vampire bat *Desmodus rotundus* roosts, the relatedness and genetic structure within female groups remains effectively independent of resident males (Wilkinson 1985b). Additionally, extra-group copulations are expected to reduce within-group relatedness (Sillero-Zubiri et al. 1996). Gagneux et al. (1999) suggest that low relatedness between philopatric male chimpanzees in the Tai Forest results from high levels of extra-group copulations. Finally, if individuals gain reproductive success during temporary tenure of high dominance positions (Wilkinson 1985b; Altmann et al. 1996) the result may be genetic structure within and between cohorts.

Patterns of genetic structure may be further complicated when the social units form part of a metapopulation. In this case the frequency of turn-over events and critically the size and kin-structure of founder groups, will have an important influence upon genetic variation (Whitlock and McCauley 1990; Whitlock 1992; Whitlock 1994).

5.1.3 Coloniality, dispersal and genetic structure in the sociable weaver

Maclean (1973) predicted that the strict sociality together with infrequent dispersal would lead to genetic differentiation between sociable weaver colonies. However, the relatively frequent occurrence of inter-colony dispersal described in this study (chapter 4) suggests there is unlikely to be genetic differentiation between colonies.

Several other predictions can be made concerning the ways in which coloniality is expected to influence genetic structure in the sociable weaver. First, as colonies impose tight spatial definitions, philopatry implies maintaining membership of a small social group. Therefore, if philopatry is biased towards males, as is common in birds (Greenwood 1980), average intra-colony relatedness is predicted to be

relatively high amongst adult males (Chesser 1991a,b). Second, this is predicted to be especially true for males living at small colonies with few breeding lineages (Chesser 1991a; De Ruiter and Geffen 1998). Third, if average dispersal distance is short (chapter 4) then colonies are expected to exchange most migrants with their close neighbours. In conjunction with high philopatry, this is predicted to mean that average inter-colony relatedness decreases with increasing inter-colony distance.

5.2 AIMS

The main aim of this chapter is to describe the consequences of coloniality for the genetic structure of the sociable weaver. This is divided into three sub-aims:

(1) To determine whether there is a sex bias in the occurrence of natal philopatry in the sociable weaver.

(2) To test Maclean's (1973) prediction that there is significant genetic differentiation between sociable weaver colonies.

(3) To use estimates of relatedness to test three hypotheses of genetic structure: (a) that average relatedness within colonies is higher for the philopatric sex; (b) that average relatedness within colonies decreases with colony size; (c) that relatedness between colonies decreases as a function of their distance apart.

5.3 METHODS

5.3.1 Sex differences in natal philopatry

In order to assess the rates of natal philopatry of male and female sociable weaver fledglings, the recapture records of all birds fledged from study colonies (i.e. those colonies at which all nestlings were ringed) in the austral summers of 1996 (n = 7 colonies) and 1997 (n = 7 colonies) were checked for natal and non-natal recapture (chapter 1; chapter 4). The sex of all fledglings and adults were determined using the molecular method of Griffiths et al. (1998) described in detail in chapter 2. These data were then used to calculate the frequency of natal philopatry for males and females.

5.3.2 DNA Profiling

Microsatellite profiles were determined at four loci (Pdo1, Pdo3, Pdo 4 and Pdo5) using PCR amplification and silver staining (chapter 2). Because a size marker (50 bp ladder) was run after every 12 samples on every gel, absolute allele sizes could be determined and data combined across different gels. However, because of difficulties with accurately sizing PCR products, Pdo4 was excluded from the analyses presented in this chapter. The colonies used in the analysis of genetic structure (n = 16) are shown in Figure 5.1.

5.3.3 Test of genetic differentiation

An exact test (Raymond and Rousset 1995) using genotypic data (Goudet et al. 1996) was used to test for genetic differentiation between colonies. The test, carried out using ARLEQUIN 1.1, compares the observed distribution of genotypes (a table of the frequency of k genotypes in r populations) against possible permutations of the r by k table.

5.3.4 Estimation of relatedness

The Queller and Goodnight (1989) index of relatedness (R) was used to estimate kinship. The index, which calculates a regression measure of relatedness among and between groups of individuals, is defined (Queller and Goodnight 1989) as:

$$R = \frac{\sum_x \sum_k \sum_l \left(P_y - P^*\right)}{\sum_x \sum_k \sum_l \left(P_x - P^*\right)} \qquad (5.2)$$

where l indexes allelic position (i.e. 1 or 2) at the kth locus (1, 2 or 3 in this study) for the xth individual in the data set. The ratio is calculated using P_X, the frequency within the current, xth, individual of the allele found at the lth position of the kth locus, P_y, the frequency of the same allele in the xth individual of the group with which x is being compared and P*, the frequency of the allele in the population at large. Thus, in the terms of Hamilton's rule (1964a), the numerator is equal to the sum, over all potential beneficiaries of altruism, of alleles that are identical by descent to those of their potential altruists and the denominator is equal to the sum, over all potential altruists, of alleles identical by descent to their own genotype; the number of matches in alleles between individuals (M_{xy}: Blouin et al. (1996)) weighted by the frequency of those alleles to give an unbiased estimate of true

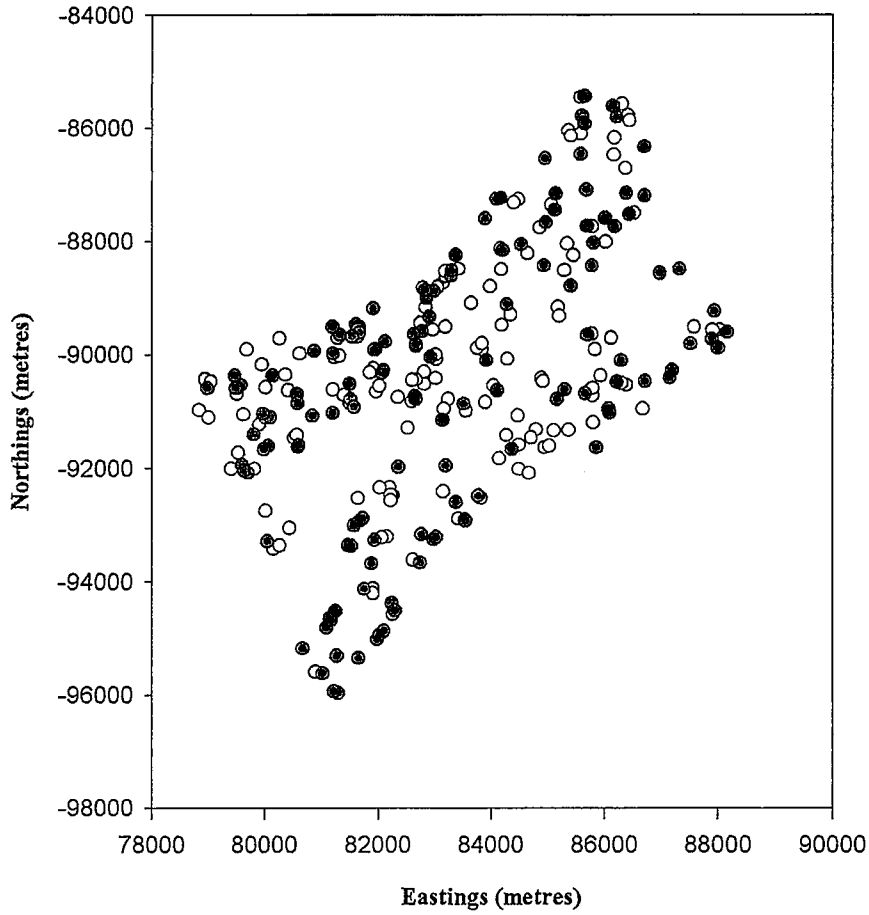


Figure 5.1 Microsatellite DNA profiles were established for 183 adult birds from 16 colonies using blood samples collected during the 1997-1998 field season. The colonies used during this investigation of genetic structure are shown as red filled circles. Active and inactive colonies (1998) which were not used are shown as blue filled and empty circles respectively. Distances are metres North and East of the point 16.000° E, 22.000° S.

relatedness ranging from -1 to 1. All values calculated in this study were symmetric (i.e. all individuals were both potential altruists and beneficiaries).

As biological interest in this study focused on the colony, in most cases relatedness estimates were calculated for groups of individuals (Queller and Goodnight 1989; Queller et al. 1993). For the calculation of average relatedness within a colony the numerator is the sum over all colony members of alleles identical by descent with other colony members and the denominator is the sum over all colony members of alleles identical by descent with their own genotype. While for the calculation of relatedness between two colonies, the numerator is an estimate of the sum over all individuals (both colonies) of alleles identical by descent with those of members of the other colony and the denominator is an estimate of the sum of alleles identical by descent with their own genotype. All estimates of relatedness within and between colonies were calculated using RELATEDNESS 5.0.4 (Queller and Goodnight 1989). Standard errors of R were calculated by jacknifing over loci by the programme (Sokhal and Rolf 1981; Queller and Goodnight 1989).

However, to calibrate the estimates of relatedness (Girman et al. 1997; De Ruiter and Geffen 1998) and perform Mantel tests (Manly 1997) it was necessary to calculate pairwise estimates of relatedness between some dyads of individuals (Queller and Goodnight 1989). This was achieved using RELATEDNESS 5.0.4 (Queller and Goodnight 1989). Standard errors were then calculated by jacknifing over loci or colonies as appropriate (Sokhal and Rolf 1981; Queller and Goodnight 1989).

In order to determine if the estimates of relatedness accurately described kinship, Queller and Goodnight (1989) values were calculated for dyads of known kinship (based upon behavioural observations and the genetic exclusion of extra-pair and brood parasite offspring: chapter 2). The mean relatedness estimate between full sibs, and between parents and offspring, was expected to be 0.5. Between half sibs it was expected to be 0.25. As only three loci were typed, a rarefaction analysis of the relatedness estimates was not attempted (see: Altmann et al. 1996; Girman et al. 1997; De Ruiter and Geffen 1998).

5.3.5 Tests of population structure using relatedness estimates

(a) Relatedness within colonies: sex differences

Having calculated pairwise estimates of relatedness for all sampled adult (1998) dyads Mantel tests were used to test for statistical differences in relatedness within and between colonies for males and females. The Mantel test of correlations

between matrices, was used as relatedness estimates are non-independent (Dietz 1983; Manly 1985; Manly 1997). The correlation between a matrix of dyadic relatedness estimates (for males: n = 96 birds, 4560 estimates of relatedness, 15 colonies; for females: n = 84 birds, 3486 estimates of relatedness, 13 colonies) and a matrix of colony membership statii (equal to the reciprocal of (same sex colony size - 1) if both members of the dyad lived at the same colony (Zimmerman et al. 1985; Manly 1997), zero if they did not) was examined. Calculations were carried out using GENETIX (Belkhir et al. 1998) with 10,000 permutations.

The same approach was used to test if males or females living in the same nest mass at colony 2 (chapter 2) were more related than expected by chance (for males, n = 13 birds, 10,000 permutations; for females, n = 6 birds, 720 permutations).

(b) Relatedness within colonies: colony size

The relationship between average estimated relatedness within colonies (for all males, all females, all individuals and all opposite sex individuals) and colony size was investigated using Spearman's rank correlation coefficient. Fifteen colonies were used in the analysis for males (one colony was excluded as only one male was sampled). Thirteen colonies were used in the analysis for females (at one colony no females were sampled and at two colonies only one female was sampled). All sixteen colonies were used in the analysis for all individuals and fifteen were used in the analysis for opposite sex individuals.

(c) Relatedness between colonies

In order to determine if, as predicted, average relatedness for all adults between colonies decreased with distance apart, the correlation between inter-colony relatedness estimates and inter-colony distances (chapter 4) was tested with a Mantel test as suggested by Luikart and England (1999). Fourteen colonies (all with five or more sampled adults) were used in the analysis which was carried out with 10,000 permutations using GENETIX (Belkhir et al. 1998).

5.4 RESULTS

5.4.1 Sex differences in natal philopatry

Of the 35 birds fledged in 1996 none were recaptured in either 1997 or 1998. However, of the 88 birds fledged in 1997, 20 (23%) were recaptured at their natal colony structure. In addition three birds were recaptured at a new colony along with adults from their natal colony (44% (7 of the 16) adults captured at colony 15

in the 1997 field season were recaptured at colony 12 (distance 1300 m) in 1998). Thus approximately 26% (23 out of 88) of fledglings remained in their natal group.

Sex was determined for 74 of the 88 birds fledged in 1997; 37 were male and 37 female. The frequency of recapture of males was higher than that of females at the natal colony (Figure 5.2; males: 12 out of 37 philopatric, females: 4 out of 37 philopatric; $Chi^2 = 3.91$, $df = 1$, $p < 0.05$) and the natal group (males: 15 out of 37 philopatric, females: 4 out of 37 philopatric; $Chi^2 = 7.08$, $df = 1$, $p < 0.01$). Therefore, on average male birds were three to four times more likely to remain philopatric than females.

5.4.2 Test of genetic differentiation

There was no evidence of genetic differentiation between the surveyed colonies (P(non-differentiation) = 0.834) using Raymond and Rousset's (1995) exact test. In other words, the frequency of genotypes does not vary significantly between colonies.

5.4.3 Estimation of relatedness: calibration

The Queller and Goodnight (1989) index gave estimates in the range of the expected values for the dyads of known kinship (Fig 5.3; full sibs: $R_{OBS} = 0.55 \pm 0.06$, $n = 30$ dyads, $R_{EXP} = 0.5$; parent-offspring: $R_{OBS} = 0.40 \pm 0.07$, $n = 118$ dyads, $R_{EXP} = 0.5$; half sibs: $R_{OBS} = 0.13 \pm 0.07$, $n = 17$ dyads, $R_{EXP} = 0.25$; unrelated (males at colonies 2 and 31): $R_{OBS} = -0.02 \pm 0.01$, $n = 192$ dyads, $R_{EXP} = 0$). Therefore, the Queller and Goodnight (1989) values provide relatively good estimates of the expected kinship values.

5.4.4 Tests of population structure using relatedness estimates

(a) Relatedness within colonies: sex differences

The average intra-colony relatedness for adult males (average over 15 colonies of mean pairwise intra-colony relatedness estimates) was 0.09 ± 0.02 (Fig 5.4; $n = 15$ colonies). The average inter-colony relatedness (mean pairwise inter-colony relatedness estimate) for males was 0.00 ± 0.01 (Fig 5.4; $n = 4180$ dyads). For females the average intra-colony relatedness was 0.00 ± 0.01 (Fig 5.4; $n = 13$ colonies) and the average inter-colony relatedness was 0.01 ± 0.01 (Fig 5.4; $n = 3439$ dyads).

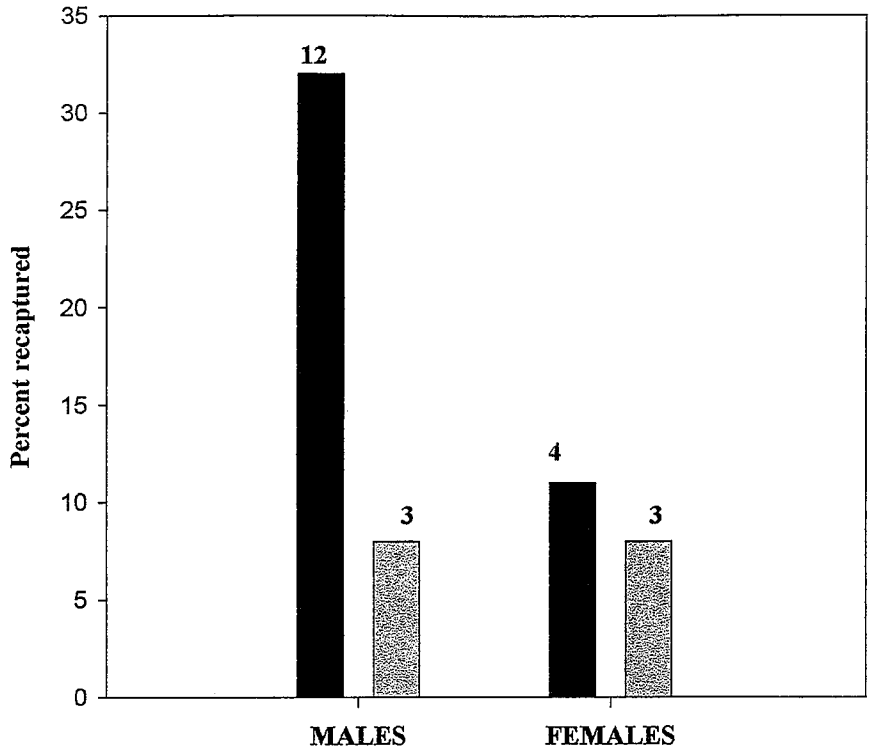


Figure 5.2 Percentages of known sex fledglings subsequently recaptured at natal (black bar) and non-natal (grey bar) colonies. There was a significant difference in the proportion of birds remaining philopatric between males and females ($\chi^2 = 3.91$, df = 1, $p < 0.05$).

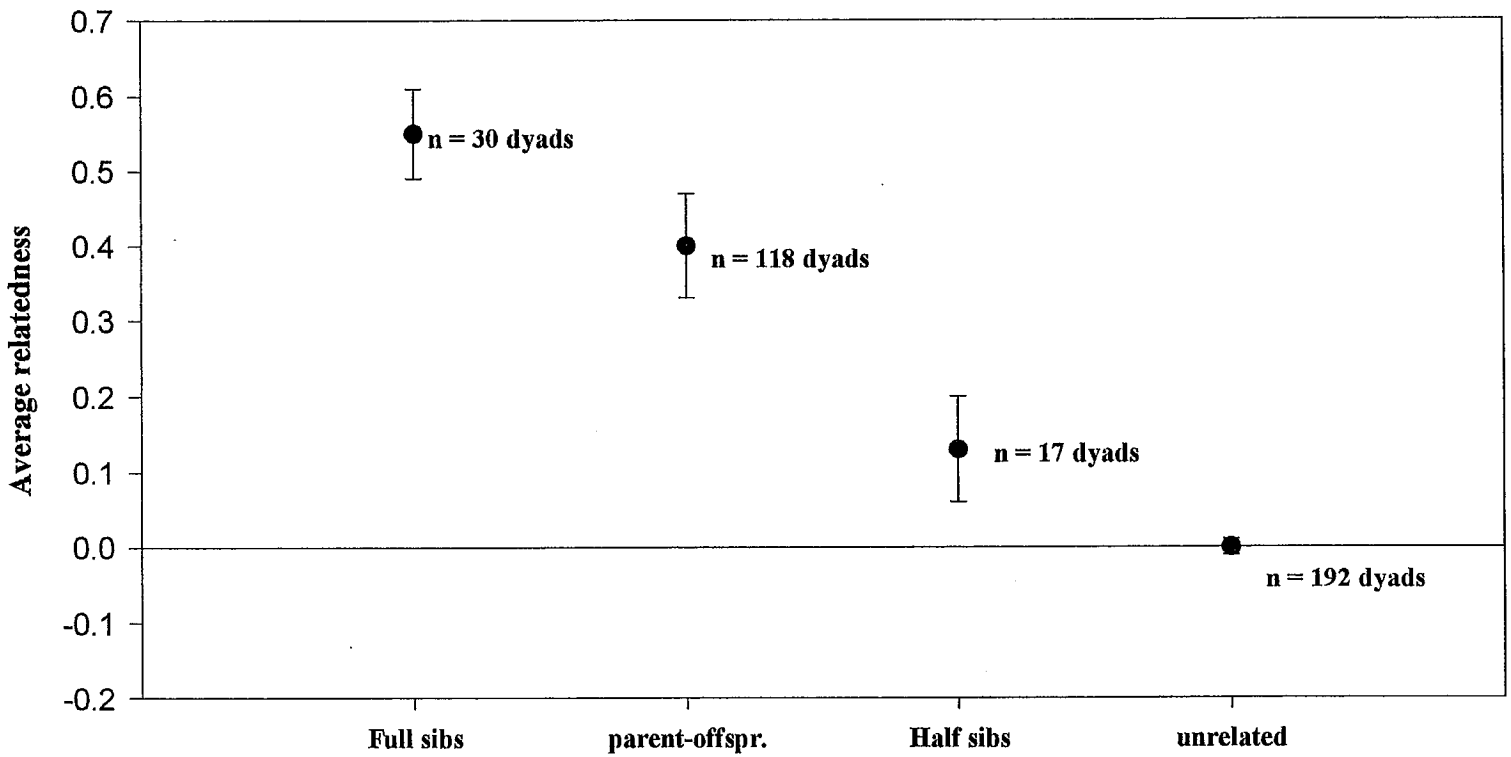


Figure 5.3 Mean estimated coefficient of relatedness values for four different classes of known kinship (the expected values are: 0.5 for full sibs and parents-offspring, 0.25 for half sibs and 0 for unrelated individuals). The number of dyads used for each estimate are shown. Standard errors were calculated by jacknifing over the three microsatellite loci.

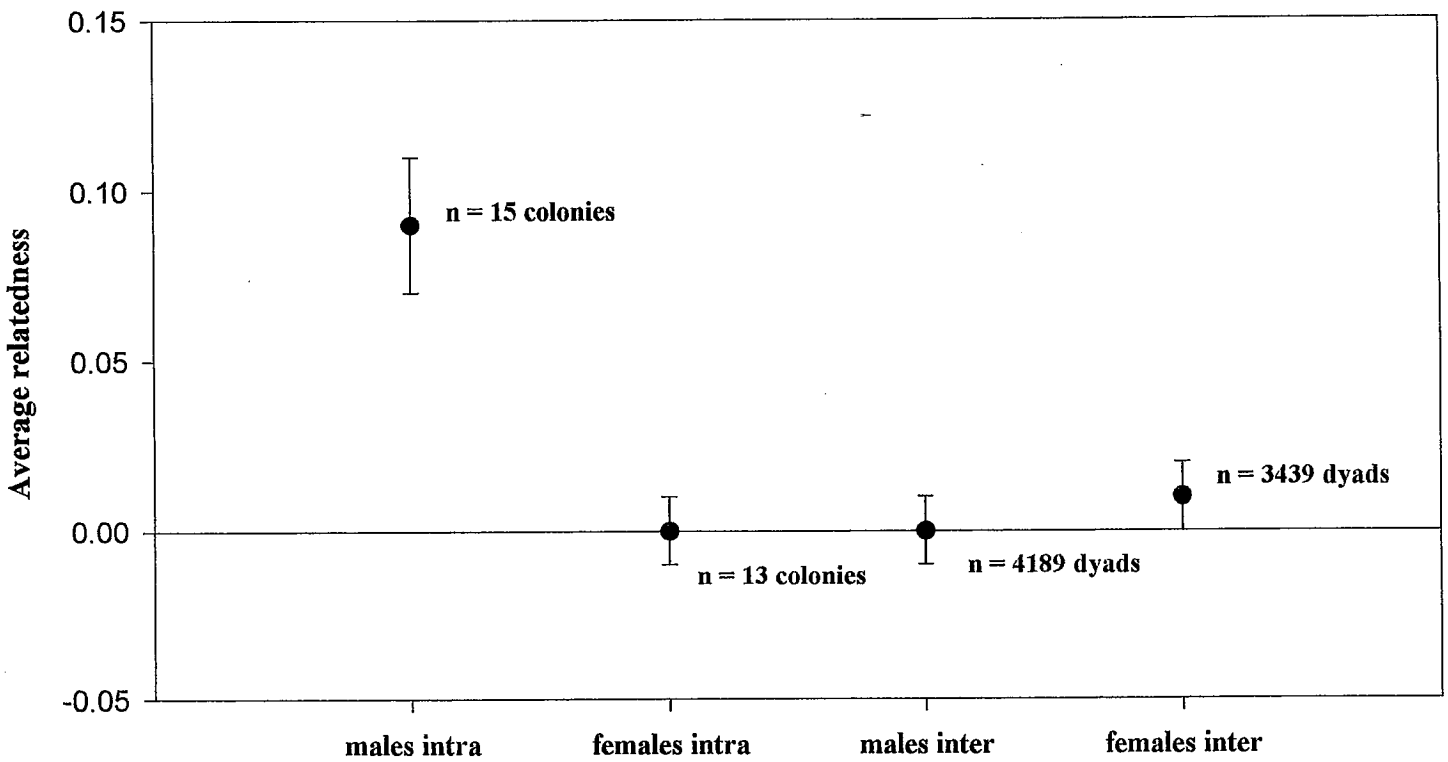


Figure 5.4 Mean estimated intra- and inter-colony relatedness colony for males and females. The intra-colony value was calculated as the average over colonies of mean values for dyads living at the same colony. The inter-colony value is the average over dyads living at different colonies. Statistical analysis is presented in the text (Section 5.4.4.i). Standard errors were calculated by jacknifing over three microsatellite loci.

For males, but not females, average intra-colony relatedness was significantly different from inter-colony relatedness (males: MANTEL TEST, Z = 5.19, E(Z) = 0.47, $p < 0.001$; females: MANTEL TEST, Z = 0.63, E(Z) = 0.5890, p = 0.474).

However, there was no significant difference in pairwise estimates of relatedness between birds living at the same and different nest masses at colony two (males: MANTEL TEST, Z = -0.89, E(Z) =-0.7633, p = 0.349; females: MANTEL TEST, Z = -0.38, E(Z) = -0.28, p = 0.153).

(b) Relatedness within colonies: colony size

There was a non-significant trend of decreasing average relatedness between adult males with increasing adult male population size (Fig 5.5.a; $r_s = -0.453$, $p < 0.1$). But, average relatedness between adult females did not vary with adult female population size (Fig 5.5.b; $r_s = 0.030$, $p > 0.5$). There was no relationship between average relatedness for all adults and total adult population size (Fig 5.6.a; $r_s = 0.265$, $p > 0.2$). However, average relatedness of opposite sex colony members significantly increased with total adult population size (Fig 5.6.b; $r_s = 0.624$, $n = 15$, $p < 0.02$).

(c) Relatedness between colonies

There was no significant correlation between inter-colony relatedness and inter-colony distance (Fig 5.7; MANTEL TEST, Z = -3969, E(Z) = -12698, p = 0.20).

5.5 DISCUSSION

Five main results are presented in this chapter. (1) Natal philopatry in the sociable weaver was male biased with males over three times more likely to remain in their natal group than females. (2) As expected there was no evidence of genetic differentiation between colonies. (3) However, there was evidence of structured patterns of adult relatedness; male relatedness within colonies was significantly greater than expected by chance. The same was not true for females. (4) There was also evidence of colony size effects on intra-colony relatedness; males within a colony were more closely related (although not significantly so) in small colonies and members of the opposite sex were more closely related in larger colonies. However, neither average female relatedness nor average relatedness for all birds varied with colony size. (5) Finally, average inter-colony relatedness did not increase with inter-colony distance; birds living in colonies which were close together were not more closely related than birds living in colonies which were far apart.

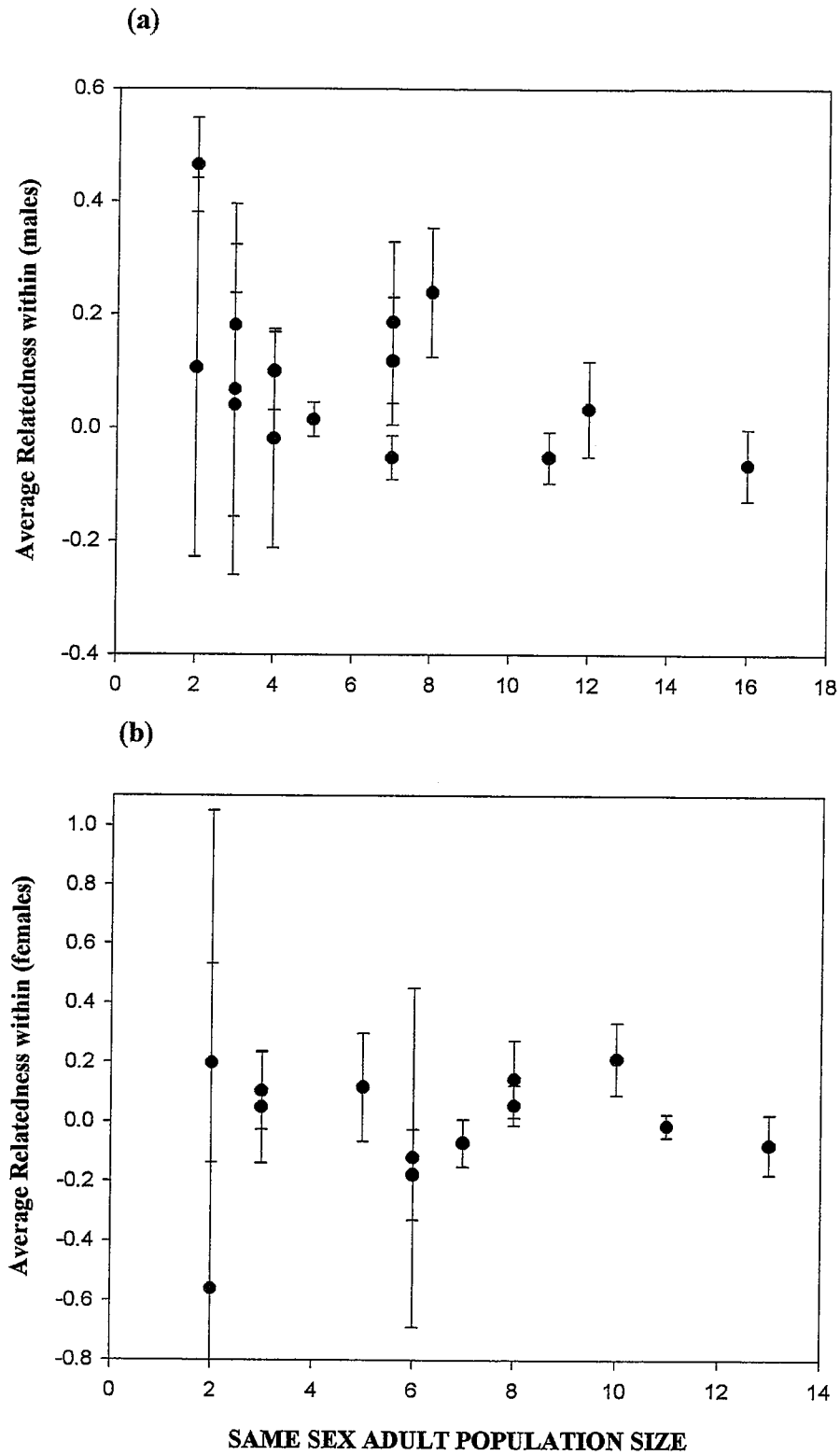


Figure 5.5 Variation in average relatedness within colonies as a function of colony size for (a) males and (b) females. There was a non significant trend of decreasing relatedness with increasing colony size for males ($r_s = -0.453$, $n = 15$, $p < 0.1$). There was no evidence of a relationship for females ($r_s = 0.030$, $n = 13$, $p > 0.5$). Standard errors were calculated by jacknifing over loci.

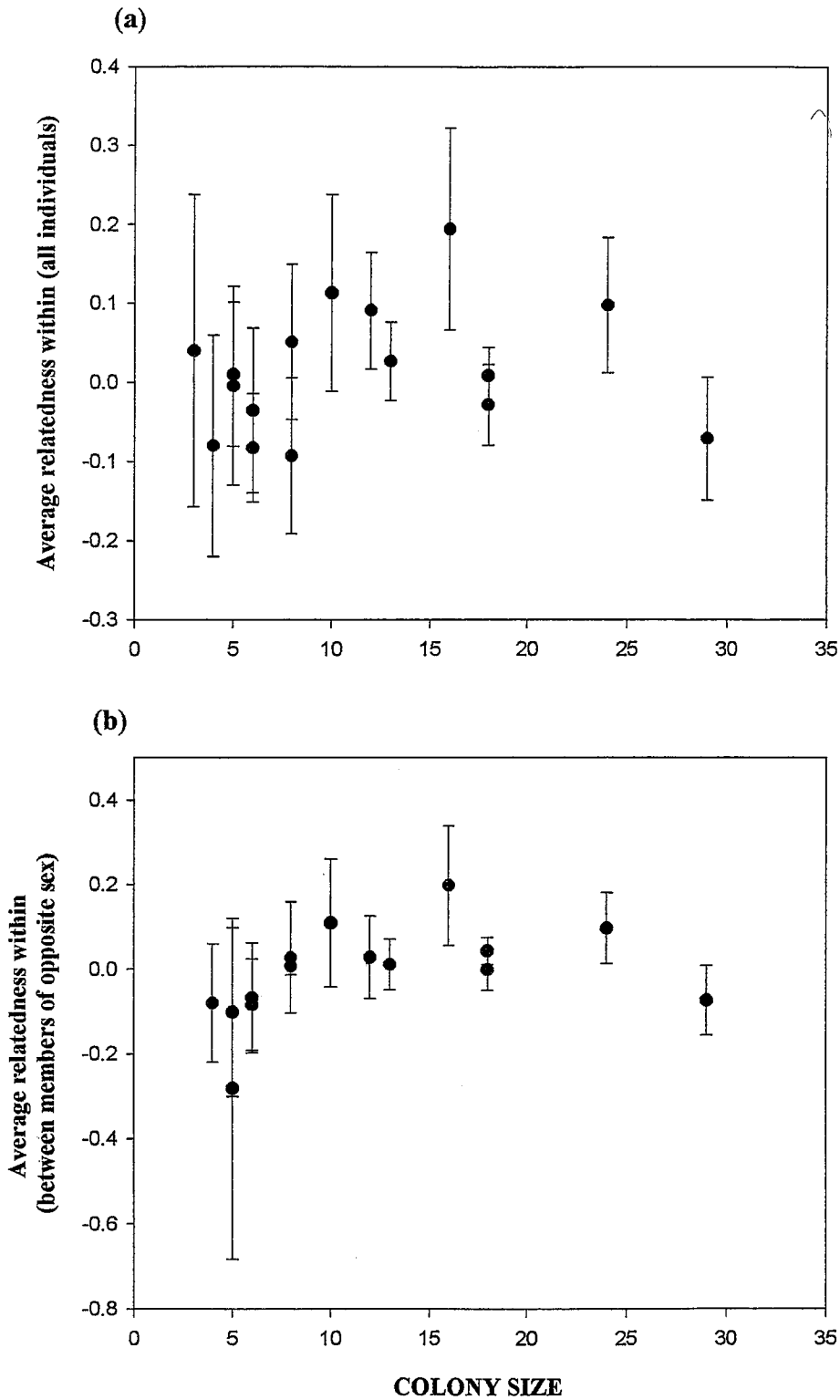


Figure 5.6 Variation in mean relatedness within colonies as a function of adult colony size for (a) all individuals and (b) all opposite sex colony members. There was no significant variation in average relatedness with colony size for all individuals combined ($r_s = 0.265$, $n = 16$, $p > 0.2$). But, mean relatedness between opposite sex birds increased with colony size ($r_s = 0.624$, $n = 15$, $p < 0.02$). Standard errors were calculated by jacknifing over loci.

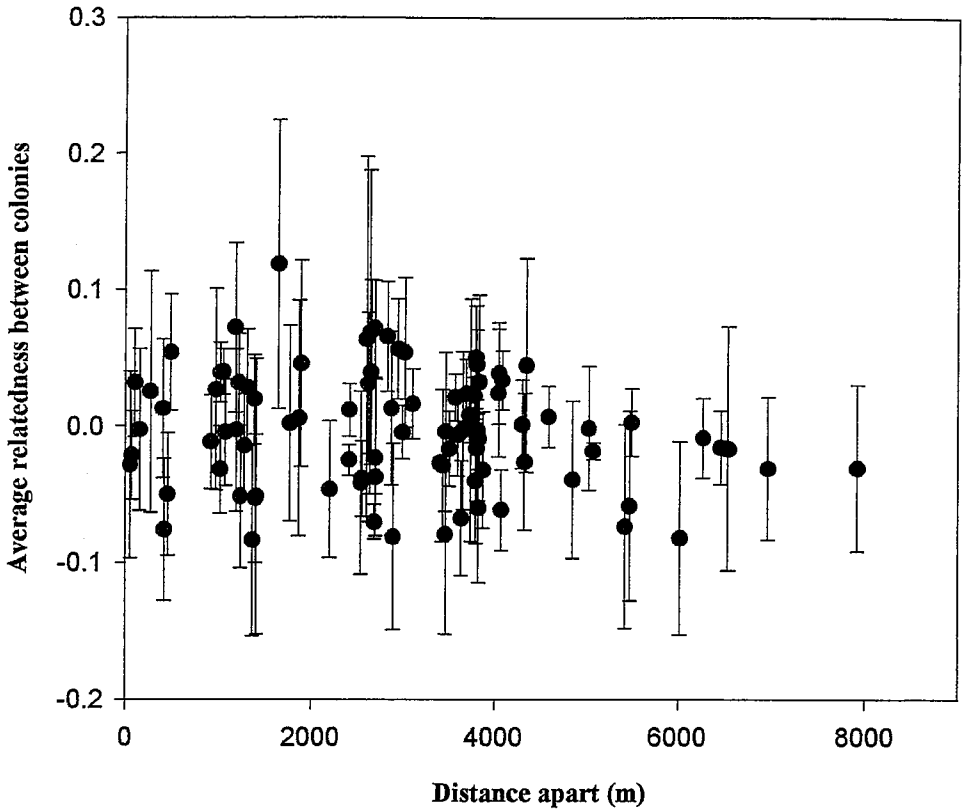


Figure 5.7 Average adult inter-colony relatedness against inter-colony distance for 14 sociable weaver colonies. There was no significant correlation between inter-colony relatedness and inter-colony distance (Mantel test: n = 14 colonies, Z = -3969, E(Z) = -12698, p = 0.20). Standard errors were calculated by jacknifing over loci.

5.5.1 Relatedness: validity of results

The estimates of relatedness presented in this chapter are based on a small number of microsatellite loci and are therefore likely to be imprecise (Altmann et al. 1996; Blouin et al. 1996). However, the aim of this chapter was to compare relative kinship estimates between groups (Queller and Goodnight 1989) rather than, for example, to make precise dyadic estimates of relatedness in order to discriminate kinship classes (Blouin et al. 1996). The callibration values confirm that although the relatedness estimates are not precise (section 5.4.3; but none are more than two standard error intervals from the expected values) they do follow the predicted pattern relative to each other; mean estimated relatedness values between full sibs and between parents and offspring are greater than the mean estimated value between half sibs which is greater than that between birds believed to be unrelated. Therefore, it can be argued that while the estimates would be unsuitable for a more detailed analysis they are reliable within the context of the aims of this chapter.

5.5.2 Genetic structure

The lack of genetic differentiation between colonies (section 5.4.2) is an expected consequence of relatively frequent natal dispersal (chapter 4). However, for the sociable weaver, as has been demonstrated for several other species (Morin et al. 1994; Webb et al. 1995; Altmann et al. 1996; De Ruiter and Geffen 1998), behaviour influences patterns of relatedness.

Dispersal was not equal for the two sexes (males were more philopatric than females) and as is predicted (Chesser 1991a,b) this asymmetry had consequences for relatedness; males but not females were significantly more related within than between colonies. Furthermore, there was a trend of negative correlation between male intra-colony relatedness and colony size (Chesser 1991a). This suggests that while small colonies tend to be composed of a single patriline, leading to high average male relatedness ($R = 0.2\text{-}0.4$), larger colonies include several patrilines and thus have low average male relatedness ($R \approx 0$). This effect may be multiplied as smaller colonies are likely to have been extinct (and hence recolonized) more recently (Chapter 4) so their resident males may be related through a recent common ancestor. The third result of interest was that dispersal appears to be sufficient to prevent structuring of adult relatedness between colonies. Although the mean natal dispersal distance for sociable weavers reported in chapter 4 was short (404m), genetic studies using mtDNA suggest that occasional long distance gene flow (upto 1000 km and over water barriers) occurs in sedentary cooperative breeders

(Edwards 1993a,b) and so it is not surprising that this sociable weaver population is less viscous than it appears on the basis of limited dispersal data.

Dispersal is not the only behaviour expected to influence patterns of relatedness. Of particular interest are extra-colony copulations (chapter 2) which might increase gene flow between adjacent colonies (Gagneux et al. 1999). Unfortunately, insufficient data were available on paternity (and especially assigned extra-pair paternity) to investigate the influence of patterns of reproductive success upon genetic structure (Scribner et al. 1993).

Environmental variation may also play an important role in determining patterns of relatedness. The data presented in this chapter describes the pattern of natal philopatry for the period April 1997 to December 1997 and the genetic structure of the study colonies for March/April 1998. However, there is probably stochastic variation in factors such as reproductive success (Appendix 1), rates of dispersal (no recruitment was recorded at natal colonies was recorded for chicks fledged in 1996), and patterns of colony extinction between years. As this variation is expected to create concurrent variation in genetic structure, the results presented in this chapter can be thought of as a single episode in a long running soap opera.

5.5.3 Genetic structure and behaviour

(a) social behaviours

Intra-colony male relatedness was greater than expected by chance in the sociable weaver. However, in absolute terms the value was not large (R = 0.09; between the values for half sibs and unrelated birds) and was partially dependent for significance upon the much higher values reported in small (up to eight adult males) colonies. The average value was similar to that reported within social groups for long tailed macaques (De Ruiter and Geffen 1998: all individuals, R = 0.10), vampire bat roosts (Wilkinson 1985b: females, R = 0.1 or less) or within burrow clusters for northern hairy nosed wombats, *Lasiorhinus krefftii* (Taylor et al. 1997: males, R = 0.052; females R = 0.092) but low compared to values reported for wild dog packs (Girman et al. 1997: males, R = 0.351; females, R = 0.276) or high rank long tailed macaque matrilines (De Ruiter and Geffen 1998: R = 0.30-0.47).

In order for an average relatedness between males of 0.1 to favour the evolution of an altruistic behaviour the benefit of the behaviour would need to be at least ten times the cost (equation 5.1). Due to difficulties estimating costs and benefits it is uncertain which behaviours would satisfy this criterion. While it might be interesting to consider sexual differences in behaviour in this context (Maclean

1973; Collias and Collias 1978; Chapter 2; males nest build more, spend more time at the colony, mob lovebirds *Agapornis roseicollis* more), many other factors will influence these differences (Harvey and Bradbury 1991; Clutton Brock 1991; Davies 1991; Andersson 1994) so the formulation of testable hypotheses would be difficult.

Average relatedness within social sub-structures of a large colony may be much higher than that described for the whole colony. For example, if colonies are divided into patrilines, relatedness within patrilines may be high (and possibly equivalent to that found in small colonies). If this is the case then, subject to some form of kin discrimination (Sherman et al. 1997), altruistic behaviours may be expected to evolve. A preliminary investigation of the relationship between behaviour and genetic structure demonstrated that individuals living at the same nest mass at colony two were not more closely related than those living in different nest masses. But many other forms of social behaviour in the sociable weaver deserve attention. For example the relationship between kinship and the frequency with which pairs of birds provision young (cooperative breeding, see chapter 2), forage or mob intruders together should be investigated.

(b) Inbreeding avoidance

The sedentary habit of many cooperatively breeding birds creates the potential for incestuous matings (Thornhill 1993; Rowley et al. 1993). The consequence of such matings (inbreeding) for fitness in natural populations is far from clear (Reeve et al. 1990; Rowley et al. 1993; Keller et al. 1994; Keane et al 1996) although there is evidence that some species actively avoid inbreeding (Koenig et al. 1998) or minimise it at the level of breeding groups (Dobson et al. 1997). In the sociable weaver, average relatedness between opposite sex individuals was positively correlated with colony size. This suggests that in small colonies inbreeding avoidance occurs as a result of the genetic structure of the population, while in larger colonies if mating is random then some weak inbreeding may be expected. However, if inbreeding avoidance does occur the situation is probably more complex. As a first simplification, the three potential incestuous first order pairings are brother-sister, father-daughter and mother-son. While natal female dispersal (although it is not complete; around 10% of females remain philopatric) will reduce the probability of the brother-sister and father-daughter pairings, avoidance of mother-son matings could be achieved only by some form of kin discrimination. Thus, the sociable weaver represents a good candidate species for a detailed investigation of the occurrence of incestuous pairing and, if it less frequent than expected by chance, the mechanism by which it is avoided.

5.5.4 Conclusions

Although there is no evidence of genetic differentiation between sociable weaver colonies, sex differences in natal philopatry correspond with patterns of adult relatedness. Thus, behaviour in the sociable weaver appears to influence genetic structure. The implications of this genetic structure for the occurrence of altruistic (and other) behaviours deserves future attention.

CHAPTER 6: GENERAL DISCUSSION

6.1 MAIN FINDINGS

The main aim of this thesis was to investigate the correlates of coloniality in the sociable weaver. Six main findings were presented:

(1) As described by Maclean (1973) much sociable weaver behaviour is centred around the communal nest. Males and females differ in their patterns of social behaviour. Males spend more time at the nest. They also add to the nest mass, mob lovebirds, and act aggressively more frequently than females.

(2) The occurrence of cooperative breeding was confirmed in the sociable weaver. Slightly under half of sociable weaver broods were fed by three adults. In all cases these trios were composed of two males and a female. In each case, only one of the males gained paternity of within-group offspring. It was not possible to determine the degree of kinship between group members. Based on the limited sample size available, there was no difference in reproductive success (measured as total number of fledglings per group) between pairs and trios. There was however, an intriguing effect on provisioning rate. In pairs there was no difference in the provisioning rate of males and females but in trios the male with paternity fed significantly less frequently than the female.

(3) Both intra-specific brood parasitism (11 % of clutches; 6 % of chicks) and extra-group paternity (27 % of clutches; 17 % of chicks) occurred in the sociable weaver. There was no difference in the frequency of extra-group paternity between pairs and trios.

(4) Various factors which might be expected to influence reproductive success correlated with colony size in the sociable weaver. Chicks in large colonies were lighter, snakes (important sociable weaver nest predators) visited large colonies more frequently and robbed all eggs and chicks, and adults in large colonies carried more feather lice. There was no correlation between colony size and frequency of intra-specific brood parasitism or frequency of extra-group paternity. Nor was there a correlation between colony size and fledging success (fledglings/group/breeding season). Therefore no clear benefits of coloniality were recorded in the sociable weaver during the present study.

(5) Colonial living had implications for the local-dynamics of sociable weaver colonies. During the present study colony size partially predicted the probability of

local extinction and colonization: small colonies were more likely to become extinct than large colonies; while large colony structures were more likely to be colonized than small colony structures. Contrary to expectation, the degree of isolation of colony structures did not predict the probabilities of local colonization or extinction However, for low estimates of dispersal both colony size and isolation the predicted probability of colony structure occupancy. Further, long term, studies are needed to determine the implications of this result.

(6) Colonial living and dispersal pattern had implications for the genetic structure of sociable weaver populations. Male sociable weavers showed a high level of natal philopatry (32% of male fledglings were recaptured at their natal colony) and this translated into genetic structure; males but not females were more related within than between colonies. The relatedness of males decreased (although not significantly) with colony size. Average relatedness between birds from different colonies did not vary with distance between colonies.

6.2 COLONIALITY AND THE SOCIABLE WEAVER

The aim of this thesis was to investigate the causes and consequences of coloniality in the sociable weaver bird. The findings presented in chapters two to five outline some of the impacts of coloniality upon the biology of the sociable weaver. These results are substantially discussed within the chapters. Therefore the aim of this discussion is to draw together the findings of chapters two, three and five concerning the social and genetic structure of the sociable weaver colonies and to put them into the context of other studies. Following this, some areas for future research are discussed with particular emphasis on the implications of coloniality for patterns of local population dynamics.

6.2.1 Coloniality and family living

The results presented in the present study suggest that the social organisation of the sociable weaver is complex and closely linked to their colonial lifestyle. This is of particular interest because of the emphasis which has been placed on the study of complex avian social organisation (Emlen 1982a,b, 1984, 1991, 1995, 1997; Brown 1987; Koenig and Mumme 1987; Stacey and Koenig 1990; Koenig et al. 1992). These studies provide a context within which the present study can be considered, hopefully providing a new point of departure for future studies of the unique coloniality shown by sociable weavers.

Many colonial species are non-sedentary (Wittenberger and Hunt 1985), and although little is known about patterns of kinship, it is generally assumed that colonies are aggregations of breeding pairs rather than extended family groups. For example, in the migratory cliff swallow *Hirundo pyrrhonota,* only 59% of eight thousand adult birds captured in two consecutive years bred at the same colony in both years (Brown and Brown 1996). In contrast, sociable weaver colonies appear to be composed of one or more family groups; many males remained philopatric at their natal colony and as result male intra-colony relatedness was high (especially in small colonies). Furthermore, cooperative breeding, a frequent correlate of multi-generational family groups (Emlen 1995,1997), was recorded.

If sociable weaver colonies are composed of one or more family groups then the assumption that genetic structure is a consequence of coloniality may be invalidated. A more fruitful approach for future studies of the sociable weaver may be to consider the evolution and maintenance of coloniality in tandem with the evolution and maintenance of multigenerational family groups. Family groups are likely to occur when the benefits to potential dispersers of remaining philopatric outweigh the benefits of dispersing to breed independently, or of dispersing to float (Emlen 1984, 1991, 1997; Koenig et al. 1992). This means that both extrinsic constraints on dispersal due to the scarcity of an essential resource and intrinsic benefits of philopatry or group living (Stacey and Ligon 1987) may select for the evolution of delayed dispersal (Emlen 1991; Koenig et al. 1992). In the following section the relationship between coloniality and family life is discussed in the context of these factors.

The arid savannah habitat with its unpredictable patterns of rainfall represents an important force shaping the social organisation and reproductive behaviour of the sociable weaver; rainfall constrains both reproductive behaviours and success (Maclean 1973; appendix 1); and the sociable weavers nest mass (Maclean 1973; White et al. 1975; Bartholomew et al. 1976) and physiology (Williams and du Plessis 1996) show evidence of adaptation to the harsh near-desert conditions.

There is good evidence that extrinsic ecological constraints on independent breeding delay dispersal, in many cooperatively breeding birds. Often the constraint is limited availability of essential breeding habitat, for example: patches of oak scrub for Florida scrub jays *Aphelocoma coerulescens* (Woolfenden and Fitzpatrick 1990); territories with granaries for acorn storage in the acorn woodpecker *Melanerpes formicivorus* in California (Koenig and Mumme 1987); high quality territories (with sufficient insect resources) in the Seychelles warbler *Acrocephalus sechellensis* (Komdeur 1992); breeding partners for superb fairy-wrens *Malurus*

cyaneus (Pruett-Jones and Lewis 1990 but see Rowley and Russell 1990); and nesting cavities for green woodhoopoes *Phoeniculus purpureus* (Ligon and Ligon 1990) and red cockaded woodpeckers *Picoides borealis* (Walters 1990). Where these constraints are lifted (e.g. by providing territory vacancies for Seychelles warblers (Komdeur 1992) or reproductive vacancies for superb fairy wrens (Pruett-Jones and Lewis 1990)) then dispersal increases and families do not form.

It does not seem likely that such extrinsic constraints explain the formation of family groups in the sociable weaver. Sociable weavers are colonial, they forage in large flocks, the sex ratio is close to unity and most importantly they do not defend discrete resource territories. The only obvious potential constraint on independent breeding is the availability of colony structures, yet 41% are unoccupied. However, it may be foolhardy to exclude nest masses outright. However, there is variation in thermodynamic benefits with nest mass size (larger nest masses provide more insulation (White et al. 1975; Bartholomew et al. 1976)) and large colonies are selectively colonized (chapter 4). Thus the ratio of suitable to available structures may be low. Future research is needed to determine how valuable and how limited colony structures are and to test if the degree of natal philopatry varies with the availability of colony structures (e.g. Emlen 1984 for acorn woodpeckers).

Intrinsic benefits of group living may also select for delayed dispersal (Stacey and Ligon 1987; Koenig et al. 1992). Potential benefits of group living include: reduced predation (Alexander 1974); improved foraging efficiency (Ward and Zahavi 1973; Faaborg and Bednarz 1990); improved chick rearing skills (Brown 1987; Heinsohn 1991) and improved resource defence (Packer et al. 1991; Jamieson et al. 1994). If living with relatives improves the cost/benefit ratio of these behaviours (Hamilton 1964a,b) then they will represent benefits of philopatry. The considerable variation in relatedness between dyads of individuals in large colonies may offer an insight into the importance of relatedness for sociable weaver social behaviour. As the inclusive fitness benefits of social behaviours will vary between dyads the ability to discriminate kin from non-kin should evolve (Hamilton 1964b), although the relative high rate of extra-pair paternity may limit the accuracy of learned kin discrimination. Individuals are predicted to preferentially help close relatives to provision offspring (Emlen 1990). They may also avoid mating with relatives (Rowley et al. 1993; Koenig et al. 1998), preferentially forage with relatives, cooperate with relatives when mobbing predators and show affiliative behaviour to relatives (Gompper et al. 1997; but see Keller and Reeve 1994; Emlen 1995,1997). Furthermore, when group living is closely linked to the social production and maintenance of an external resource (e.g. the sociable weavers nest mass) extrinsic and intrinsic benefits are closely linked.

During the breeding season living in large groups does not seem to improve foraging efficiency or reduce nest predation in the sociable weaver (chapter 3). However, potential non-breeding benefits for survivorship (possibly mediated through avoidance of gabar goshawk *Micronisus gabar* predation) deserve investigation.

Constraints on independent reproductive success may also be important in understanding the evolution of multi-generational families and cooperative breeding. When birds live in a variable environment, and during poor years independent reproduction is liable to fail, then the indirect fitness gained from helping may represent a benefit of philopatry. The colonially breeding white-fronted bee-eater *Merops bullockoides,* does not appear to be limited by nest sites, availability of breeding partners, or feeding territories yet dispersal is delayed and cooperative breeding common (Emlen 1990). Emlen (1990) argues that particularly for young white-fronted bee-eaters in harsh years the environment constrains independent reproductive success (e.g. the proportion of birds breeding decreases as rainfall decreases). However, as white-fronted bee eaters live in clans of relatives they may still gain indirect benefits (Hamilton 1964a; Brown 1987) from helping when breeding is not attempted or has failed (Emlen 1990).

The harsh, unpredictable environment may also act as a constraint on independent reproduction in the sociable weaver. It seems that when there is less rain, there is less food, chicks are provisioned less and reproductive success is constrained. Maclean (1973), who reported helping in a poor year but not a good year, provides anecdotal support for variation in the frequency of cooperative breeding in the sociable weaver with rainfall. Furthermore, in the closely related grey capped social weaver *Pseudonigrita arnaudi* adults live in lose colonies and when their breeding attempts finish or fail help to provision their relatives offspring (Bennun 1989; Bennun 1994) - a system similar to that described by Emlen (1990). If indirect reproduction is a benefit of philopatry then helpers are expected to (i) help their relatives (Emlen 1990; Pusey and Packer 1994) and (ii) increase the reproductive success of the breeders (Emlen 1991) - either directly through fledging success or indirectly through survival. As discussed in chapter two the data collected in the present study was insufficient for a clear evaluation of the consequences of helping in the sociable weaver. Extension of this data set is a priority for future studies.

In conclusion, coloniality in the sociable weaver appears to be a close correlate of family living and this finding should inform future investigations of coloniality and its evolution in the sociable weaver. However, because of the difficulties in

separating cause and consequence, the direction of the causal link between colonial and family life may well remain obscured (Siegel-Causey and Kharitonov 1990) and as average relatedness is not high (especially in large colonies) family living can only be one aspect of the study of sociable weaver coloniality. Despite these difficulties, understanding the evolution of multi-generational families in the context of coloniality offers an exciting challenge. Important avenues for future research include investigation of: the value and availability of colony structures; long term patterns of survival and their determinants; and perhaps most importantly patterns of helping behaviour and their consequences. More data are needed on the identities of helpers and the breeders they help, the effort invested by helpers, and the payoff from this effort both in terms the reproductive success and survival of breeders and the future reproductive success of helpers.

6.3 AREAS FOR FUTURE STUDY

Many other aspects of the biology of sociable weavers deserve further study. Of particular interest is the influence of coloniality on spatial population structures and patterns of local dynamics. Three aspects of coloniality and spatial dynamics in the sociable weaver deserve further investigation. The first area of interest is the relationship between short and long term effects in spatial dynamics (Hanski 1999). The results presented in chapter four provide a potential example of differences between long and short term patterns of spatial dynamics. While the existence of a (weak) isolation effect on occupancy but not transition frequencies may be the result of a correlation driven by habitat quality, it may also reflect the importance of environmental stochasticity for annual transition probabilities. It would be interesting to build up a longer data set in order to determine: (i) how dispersal varies between years; (ii) how colonization and extinction frequencies vary between years (Eber and Brandl 1996); (iii) the relationship between variation in dispersal and transition probabilities; (iv) if long term transition probabilities suggest the existence of an isolation effect.

The second area of interest is the relationship between patterns of behaviour and local population dynamics. At the simplest level patterns of emigration and immigration and the mechanisms by which they occur need to be defined. This includes, determination of when dispersal occurs, how dispersal occurs (are dispersers forced from their natal colony, do they prospect for new colonies, do they form social bonds when foraging flocks meet etc.), with whom dispersal occurs and what behavioural response immigrants elicite (e.g. Maclean 1973). The patterns of male and female philopatry in the sociable weaver also deserves investigation. The sociable weaver, with its high male philopatry and occasional

female philopatry (chapter 5) may represent a valuable model species in which to test hypotheses concerning when females should remain philopatric (Greenwood 1980).

A second potential area of interest is the relationship between patch system structure and population dynamics (and genetics). Variation across the sociable weavers' range (from relatively dense tree cover towards the east of their range to extremely sparse tree cover, at the edge of the Namib desert, towards the west) provides an opportunity to address the implications of the differences in the spatial distribution of colonies for patterns of spatial population dynamics and genetics and for the evolution of transfer processes (Barton and Whitlock 1997; Olivieri and Gouyon 1997; Hanski 1999). A difficulty with this approach is that differences in patch system structure are likely to be confounded by differences in rainfall, predator abundance etc. However, such research could have valuable general implications for conservation.

APPENDIX 1: REPRODUCTIVE SUCCESS AND THE ENVIRONMENT

A1.1 Aims and methods

To investigate the effect of environment variation on reproductive behaviour and success data collected during nest content checks (chapter 1) were compared between and within years in order to answer three questions:

(1) Does the timing of sociable weaver reproductive behaviour correlate closely with rainfall as reported by Maclean (1973)? This question was addressed by comparing the patterns of clutch initiation and rainfall during the three field seasons of the study.

(2) Does the reproductive effort of sociable weavers vary with rainfall as reported by Maclean (1973)? This question was addressed by comparing three measures of reproductive effort between years. The measures were mean egg volume, mean first clutch size and mean number of clutches per group.

(3) Does the reproductive success of sociable weavers vary with rainfall as reported by Maclean (1973)? This question was addressed by comparing four measures of reproductive success between years. The measures were mean hatchlings from the first clutch, mean chick mass (residual from a regression of mass against tarsus, averaged over all clutches for a group), number of fledglings from the first clutch and total fledglings per group over the breeding season.

A1.2 Results and Discussion

(1) The pattern of timing of the first clutch laid at the study site, the median date of first clutch initiation and the last date on which a clutch was initiated closely followed the pattern of rainfall at Claratal farm over the three years of the study (Fig A1.1). As only three years data were available no statistical analysis was attempted however the pattern is consistent with Maclean's (1973) observations.

(2) Year had a highly significant effect on two of the three measures of reproductive effort. Both mean first clutch size and total number of clutches over the breeding season varied significantly with year (Fig A1.2; clutch size ANOVA: $F_{2,137} = 9.06$, $p < 0.001$; total clutches ANOVA: $F_{2,142} = 23.61$, $p < 0.001$). However, mean egg volume index did not vary significantly (Fig A1.2; Egg volume ANOVA: $F_{2,136} = 1.00$, $p = 0.372$). These results suggest that sociable

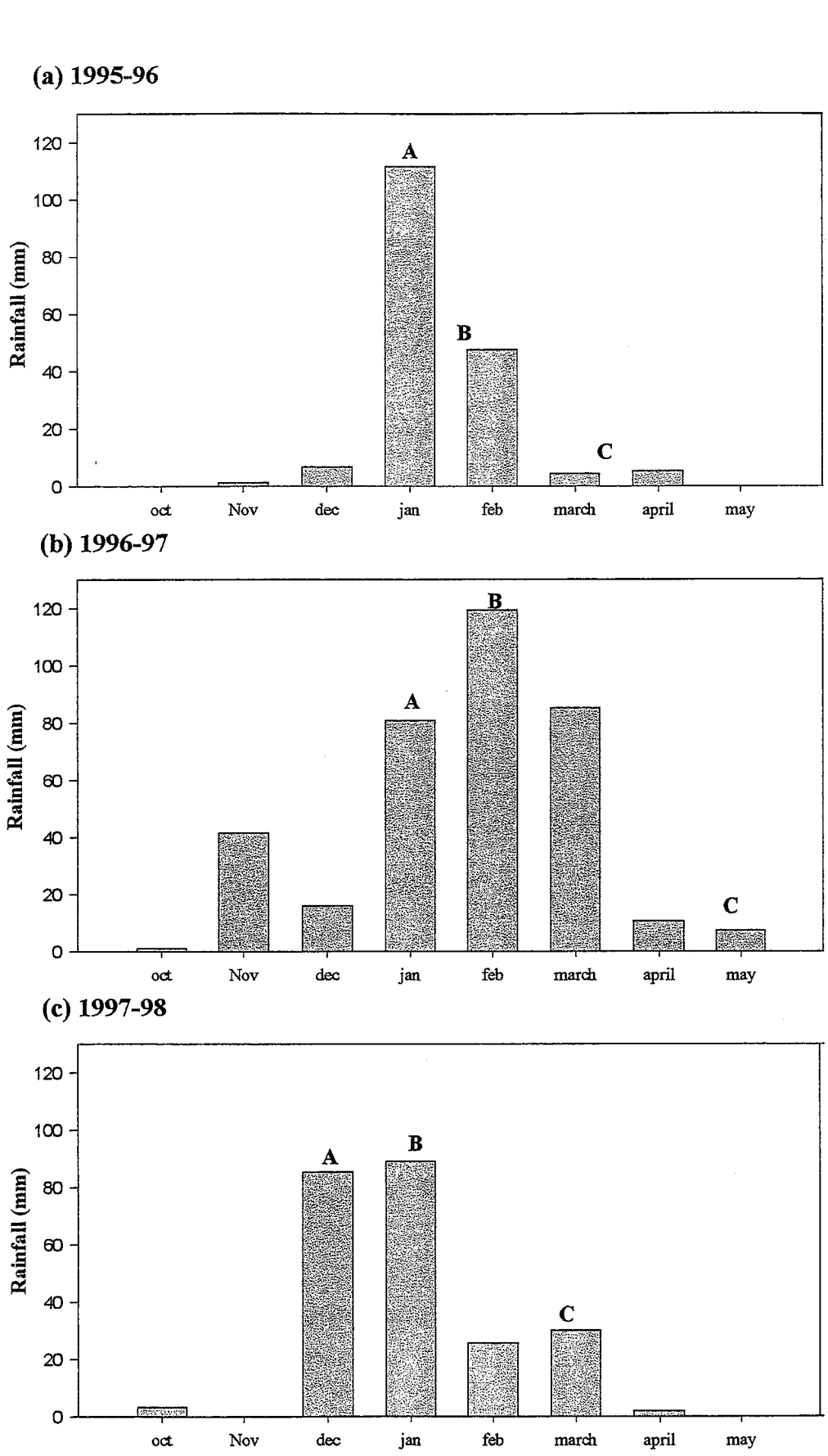
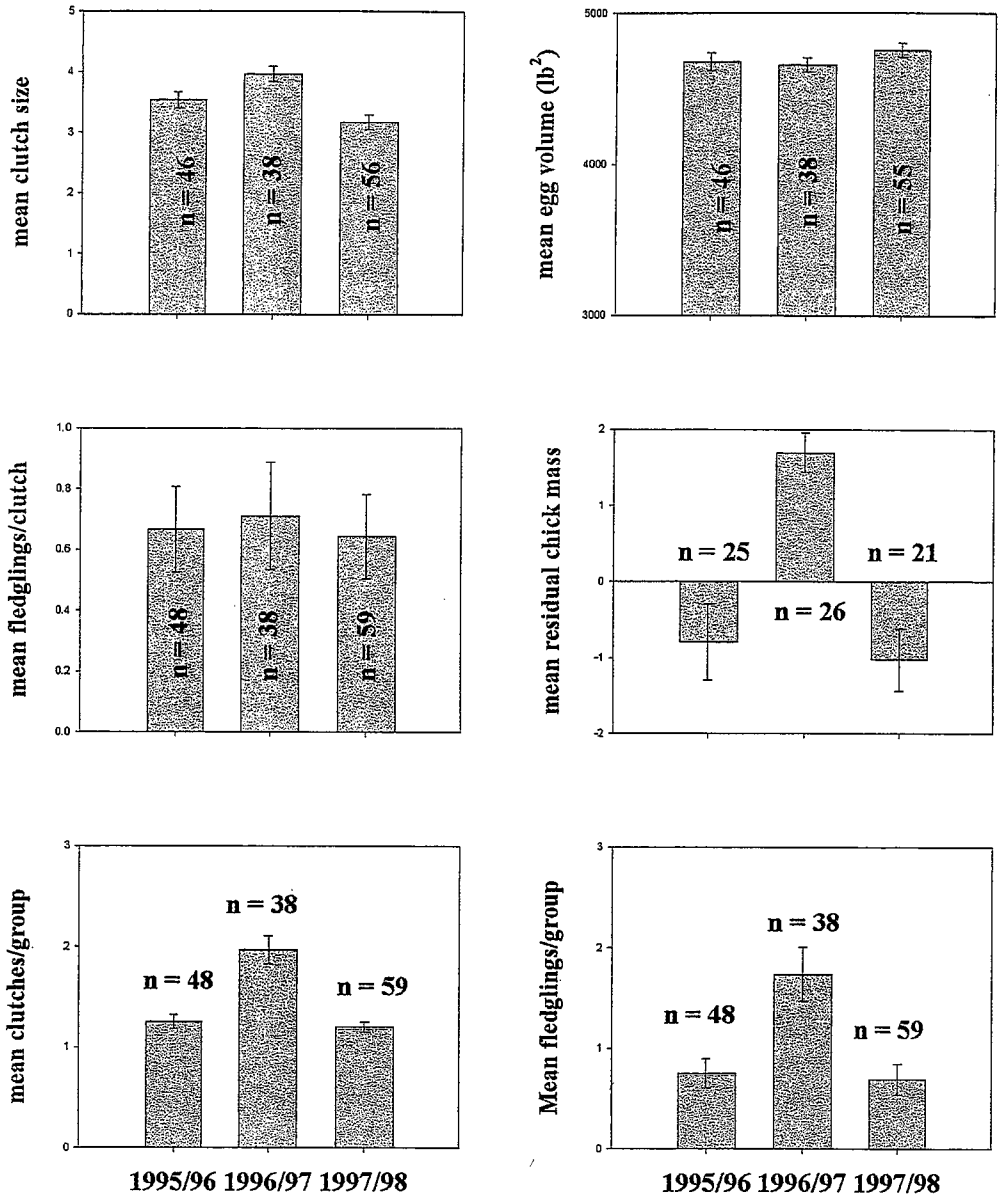


Fig A1.1 Monthly rainfall totals for (a) 1995-1996, (b) 1996-1997and (c) 1997-1998. The date of the first clutch layed (A), the median date of first clutch initiation (B) and the date of last clutch initiated (C) are indicated for each season (95/96, first: 15 January, median: 31 January, last: 26 March; 96/97, first: 16 January,median: 12 February, last: 21 April; 97/98, first: 17 December, median: 18 January, last: 7 March).



Figurte A1.2. Variation in reproductive effort and success between years. Statistics are given in the text. (i) Mean clutch size, first clutch. (ii) Mean egg volume, firstclutch. (iii) Mean number of fledglings, first clutch. (iv) Mean residual chick mass by group (regression of mass v tarsus), all clutches combined. (v) Mean number of clutches per group (vi) Mean total fledglings per group (all clutches).

weavers lay larger clutches when there is more rainfall, and more clutches when the rainy season lasts longer. This provides further evidence for the opportunistic nature of sociable weaver breeding biology (Maclean 1973).

(3) Year had a significant effect on three out of four measures of reproductive success. Mean hatchlings from first clutch, mean chick mass, and total number of fledgings all varied significantly between years (Figure A1.2; hatchlings ANOVA $F_{2,142} = 3.37$, $p = 0.037$; residual chick mass ANOVA $F_{2,69} = 14.7$, $p < 0.001$; total fledglings ANOVA: $F_{2,142} = 9.11$, $p < 0.001$). However, year did not have a significant effect on fledglings from first clutch (Figure A1.2; fledglings ANOVA: $F_{2,142} = 0.05$, $p = 0.954$). These results provide further evidence of the the importance of the environment for breeding success. The most important measure, total fledglings per group, showed a highly significant variation between years. Furthermore, the pattern of variation fits closely with the pattern of rainfall.

It is important to note that there are several difficulties with the results presented in this appendix. Perhaps the most important is that they are based on correlations using a small data set. Rainfall is not the only factor which may vary between years, for example the frequency of pairs and trios, the number of predatory snakes, the amount of available cattle fodder or the prevelance of parasites may also vary and potentially influence sociable weaver reproductive effort and success. Additionaly, total rainfall is a poor measure, the pattern of rainfall, and temperature and degree of cloud-cover (influencing evapotranspiration) will all have a role in determining plant growth and insect abundance. However, although these results are far from conclusive they are highly suggestive; sociable weavers appear to be highly opportunistic breeders, subject to pronounced variation in reproductive effort and success.

APPENDIX 2: CALCULATION OF MEAN DISPERSAL DISTANCE CORRECTING FOR RECAPTURE EFFORT

Recapture probabilities for a colonial species

The probability R of recapturing a individual which disperses upto x km from the colony where it was first captured in year t is:

$$R = \frac{\text{number of colonies ringed in year (t+1) upto distance x}}{\text{total number of colonies upto distance x}}$$

For simplicity, dispersal distances were divided in to 6 classes (0 km (i.e. birds recaught at the same colony), 0-1 km, 1-2 km, 2-3 km, 3-4 km and 4-5 km; 1 km was arbitarily chosen as the increment for each distance class). Five kilometers was used as the boundary of the sampling area as no ringed colonies were more than five kilometers apart (max = 4.8 km). Any birds dispersing more than 4.8 km could not have been recaptured and, as such dispersal may easily occur (see Edwards (1993a,b) for a striking example of evidence of long distance dispersal in a sedentary bird), all estimates calculated in this appendix represent underestimates. For each colony at which ringing took place in 1997 (n = 7), the probability of recapturing a bird which had dispersed into a given distance class i was then calculated as R_i:

$$R_i = \frac{\text{number of active colonies ringed within distance class i in 1998}}{\text{total number of active colonies within distance class i in 1998}}$$

In all cases $R_{(0\ km)} = 1$. The observed number of active colonies (determined from the colony survey: chapter 4) were used in the calculation of $R_{(0\text{-}1\ km)}$ and $R_{(1\text{-}2\ km)}$. For the larger distances classes, as the colony survey (chapter 4) did not provide complete coverage for all focal colonies, the total number of active colonies was estimated from the observed colony density (2.2 active colonies/km^2). Mean recapture probabilities were calculated for each distance class (n = 7 colonies). The total (recaptured and not-recaptured) number of dispersers D_i in a distance class was estimated as:

$$D_i = \frac{\text{observed dispersers in distance class i}}{R_i}$$

Although this estimate of D_i is littered with assumptions it provides some correction of the raw data. Estimated values of R_i and D_i are given in Table A2.1. Estimated

Table A2.1: Values for recapture probability in distance class i, R_i and observed and estimated (D_i) numbers of dispersers into that distance class. These data were used to calculate an estimate of mean dispersal distance including a partial correction for recapture effort within the study area. An Asterix represents a value which could not be estimated as a result of the limited range of the colony survet (chapter 4).

Distance class (km)	R_i actual value based on colony survey	R_i estimated value based on mean density	Fledglings (1997) recaptured	adults (1997) recaptured	D_i - Fledglings (1997)	D_i - adults (1997)
0	1	(1)	20	49	20	49
0-1	0.33	(0.27)	1	1	3	3
1-2	0.32	(0.28)	5	7	16	22
2-3	*	0.19	1	0	5	0
3-4	*	0.14	0	0	0	0
4-5	*	0.05	0	0	0	0

mean dispersal distances were calculated using these values of D_i. The estimated mean distances (± s.e.) were 0.47 km (±0.08) for adults, 0.86 km (±0.14) for fledglings and 0.61 km (±0.06) for adults and fledglings combined.

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